Bull. nat. Hist. Mus. Lond. (Geol.) **49**(2): 99–119 Issued 25 November 1993

Productellid and Plicatiferid (Productoid) Brachiopods from the Lower Carboniferous of the Craven Reef Belt, North Yorkshire

C.H.C. BRUNTON

Department of Palaeontology, The Natural History Museum, London SW7 5BD, UK

D.J.C. MUNDY

Talisman Energy, 2400, 855 2nd Street SW, Calgary, Alberta, Canada T2P 4J9

Appendix by S.S. LAZAREV

Palaeontological Institut, Academy of Sciences, Profsoyuznaya 123, Moscow 117647, Russia, CIS

CONTENTS

Synopsis. Lower Carboniferous, mainly Asbian, productoid genera, assigned to the closely related families Productellidae and Plicatiferidae, are described from reef limestone facies in the Craven Reef Belt of North Yorkshire and elsewhere, together with discussions on their relationships to genera abroad. Within the Productellidae the evolutionary history of species of *Productina* and *Argentiproducus* is described, while in the Plicatiferidae species of *Plicatifera, Acanthoplecta, Admodorugosus* gen. nov. (based on the type species *A. cracoensis* gen. et sp. nov.) and *Geniculifera* are described. The little-known British latest Devonian to earliest Carboniferous genus *Productellina* is placed in the Productininae, as is also a new Mongolian late Devonian genus, *Dorsirugatia*, described in the Appendix.

INTRODUCTION

Brachiopods are an important biotic component of the late Viséan (largely Asbian) Cracoean reefs (see Brunton & Mundy, 1988*b*) of northern England, with productidines (represented by some 45 genera) forming 37% of brachiopods in detailed collections of almost 21,000 specimens from the Craven Reef Belt made by Mundy (1980). Contributions to the systematics, palaeoecology and distribution of some of these Cracoean productidines have been made by Brunton & Mundy (1986, 1988*a*, *b*) and Mundy & Brunton (1983, 1985).

Here we describe contemporaneous taxa belonging to the families Productellidae and the related Plicatiferidae, with species assigned to *Argentiproductus, Productina, Plicatifera, Acanthoplecta, Geniculifera*, and the new genus *Admodorugosus* (p.111). Some of these species, including *Acanthoplecta mesoloba, Plicatifera plicatilis, P. pseudoplicatilis* and *Argentiproductus margaritaceus* are familiar, if not diagnostic components of the reef biota, while the remaining are rare, poorly known or overlooked. *Argentiproductus atripoides,* a Russian species, is recognized for the first time in Britain, as is the North American genus *Geniculifera,* here accommodating *Productus keyserlingianus* de Koninck, which formerly was loosely referred to *Avonia*. A rare productellid in the Cracoean biota is *Productina* cf. *pectinoides,* providing an opportunity to redescribe the species and the difference between *Productina* and *Argentiproductus*. In so doing we have investigated the evolution of the small subfamily Productininae and its probable origins in the late Devonian genus *Dorsirugatia* and slightly younger *Productellina*. The distinctive wholly rugose plicatiferid *Admodorugosus cracoensis* gen. et sp. nov. is described herein; it is a rare component in our collections from the Craven Reef Belt, but has turned up in several museum repositories from a variety of Cracoean reef localities in England, Wales and Ireland.

A brief introduction to the stratigraphy and depositional setting of the Craven Reef Belt, together with definitions of the subfacies, is given in Brunton & Mundy (1988*b*). This paper also outlined possible pathways in productidine ontogeny with a notation which, used here, would be 1 to 3 to 5 for all species, that is from an initial pedicle attachment, via varied uses of clasping spines, to support spines in adulthood (Brunton & Mundy 1988*b*: fig. 4).

Although this study is based on the extensive collections made by Mundy from the Craven Reef Belt, we have made use of specimens from elsewhere in northern England, and beyond, in order to describe and illustrate the species more fully. Numerical and distributional data on the species here considered, together with their stratigraphical ranges (in the Craven Reef Belt) are shown in Table 1 (p.116) and Fig. 72 (p.117) respectively.

Most of the collections made from the Cracoe–Burnsall section of the Craven Reef Belt by Mundy (1980) are housed in The Natural History Museum, London (NHM), formerly the British Museum (Natural History), London, with additional material in the Liverpool Museum (National Museums & Galleries on Merseyside — NMGM). Collections by Mundy from the Malham–Settle portion of the reef belt during the resurvey by the British Geological Survey (BGS) Settle map-sheet (60) (Arthurton *et al.* 1988) are housed at Keyworth, Nottingham. Additional specimens of the species described here have been studied from existing collections (largely reef limestones) in The Natural History Museum, the British Geological Survey, the Sedgwick Museum, Cambridge, the Sheffield City Museum, and the Museum of Natural History, Paris. All the figured material, unless otherwise stated, is in The Natural History Museum, London, prefixed BMNH, followed by the registration number.

TERMINOLOGY AND CLASSIFICATION

Terminology follows the *Treatise* (Williams *et al.* 1965), but we use the following new or emended terms which are not defined by Muir-Wood & Cooper (1960) or the *Treatise* (1965):

Marginal ridges — Shell thickenings forming ridges bounding the body cavity and separating it from the ears and trail. They may include cardinal or lateral ridges, ear baffles and anterolateral subperipheral rims.

Body cavity (emended) — The main space between the valves which housed the posterior coelomic space plus the anterior mantle cavity accommodating the lophophore.

Cardinal ridges — Paired ridges extending from the cardinal process laterally along the dorsal hinge line.

Lateral ridges (emended) — Paired ridges extending from the cardinal process laterally which diverge from the dorsal hinge line.

The classification here used is not as in the *Treatise* (1965) because we find inconsistencies and difficulties in the use of that system. A new classification for the Productida is being developed by Brunton and Lazarev for use in the revised brachiopod *Treatise* now in preparation. Genera with true interareas, such as those included in the 1965 *Treatise* as Chonopectinae, will be moved from the previous Productellidae to the Strophalosioidea. Here the Productininae is moved from the *Treatise* Leioproductidae (which have deep body cavities and lack complete ribbing) to the Productellidae; the Plicatiferinae, within the *Treatise* Overtoniidae, is elevated to a family which includes the Levitusiinae, previously assigned to the Dictyoclostidae (the latter family now restricted to genera with a clear reticulate oramentation on the visceral disc).

SYSTEMATIC PALAEONTOLOGY

Synonymy lists are those involving significant taxonomical revision or major descriptions.

Superfamily **PRODUCTOIDEA** Gray, 1840.

DIAGNOSIS EMENDED. Productidines lacking true interareas. Cardinal process is posteriorly or posterodorsally directed. Commonly costellate with long trails (in younger taxa) and simple spines principally on ventral valves.

Family **PRODUCTELLIDAE** Schuchert, *in* Schuchert & Le Vene 1929.

DIAGNOSIS EMENDED. Small to medium sized productoids with shallow to moderately deep body cavities. Teeth only in Devonian genera. Ribbing variably developed or lacking,

rugae weak or lacking. Spines few, on ventral valve only.

COMMENT. In the revised *Treatise* this family is to be expanded to include at least six subfamilies, each containing several genera. It is the oldest non-ribbed family in the evolution of the Productoidea, appearing in the Emsian, but varied ribbing developed in a few subfamilies, such as the Productininae late in the Devonian. The Leioproductidae differ mainly in having deep body cavities.

Subfamily **PRODUCTININAE** Muir-Wood & Cooper, 1960.

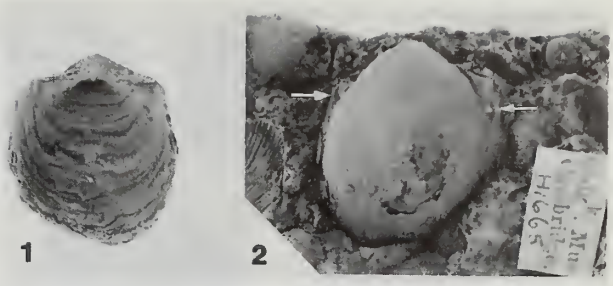
DIAGNOSIS EMENDED. Productellids with ribbing more strongly developed on ventral valves and lamellae on dorsal valves; few spines on ventral valve flanks only. Lateral ridges in both valves.

DISCUSSION. In the 1965 *Treatise* (Williams *et al.*) this subfamily contained two genera, *Productina* Sutton, 1938 and *Argentiproductus* Cooper & Muir-Wood, 1951. Brunton (1966) synonymized the two, principally because of their closely similar dorsal valve interiors. Since then several new species belonging to this group have been described from Lower Carboniferous rocks around the world, but mainly from Australia (Roberts 1976), Russia (Nalivkin 1979) and North America (Carter 1988, Rodriguez & Gutschick 1968).

Some authors (e.g. Carter, 1988) continued to recognize both genera and we now also differentiate two groups of species, attributable to *Argentiproductus* and *Productina*. The rather globose, small and relatively finely ribbed type species of *Productina, P. sampsoni* Weller, 1909 is mid Kinderhookian to early Osagian (mid to upper Tournaisian) in age, while the transverse, gently convex *Argentiproductus* type species, *A. margaritaceus* (Phillips, 1836) is from upper Viséan strata.

The earliest representative of the subfamily is probably the newly described late Devonian genus *Dorsirugatia* (Lazarev 1992, but see also Appendix, p.117, herein and listing in 1990 by Lazarev) from Mongolia. This is an inflated, but not deep-bodied, species with weak ribs not originating at the umbo, with a slightly rugose and lamellose dorsal valve, and few spines on the ventral valve only. Previously the earliest described species was *Argentiproductus rjausakensis* Nalivkin, 1979, from the uppermost Devonian of the southern Urals, closely followed by *A. dobroljubovae* Nalivkin, 1979 from the early Tournaisian of the Urals. These species are transverse in outline, with well developed ears, like *Argentiproductus,* but while the former appears to lack major spines, *A. dobroljubovae* has flanking spines. Thus it may be that here we have the last species of *Dorsirugatia* and, with the acquisition of strong spines, the first species of true *Argentiproductus*. At about the same time in North America are found specimens of *A. auriculatus* Carter, 1988, while species belonging to *Argentiproductus* extend into the Namurian, as in Algeria (Pareyn 1962).

The poorly known genus *Productellina* Reed, 1943, which has not previously been photographically illustrated, is based on two specimens of *P. fremingtonensis* Reed from the Pilton beds of north Devon. Goldring (1970) described the Fremington section in north Devon and recorded this species from his faunal divisions B and C, equated with the *Gattendorfia* and *Ammonellipsites* zones respectively. It seems, therefore, that *Productellina* appeared in the early Hastarian, Lower Tournaisian. Study of the two types in the Sedgwick Museum,

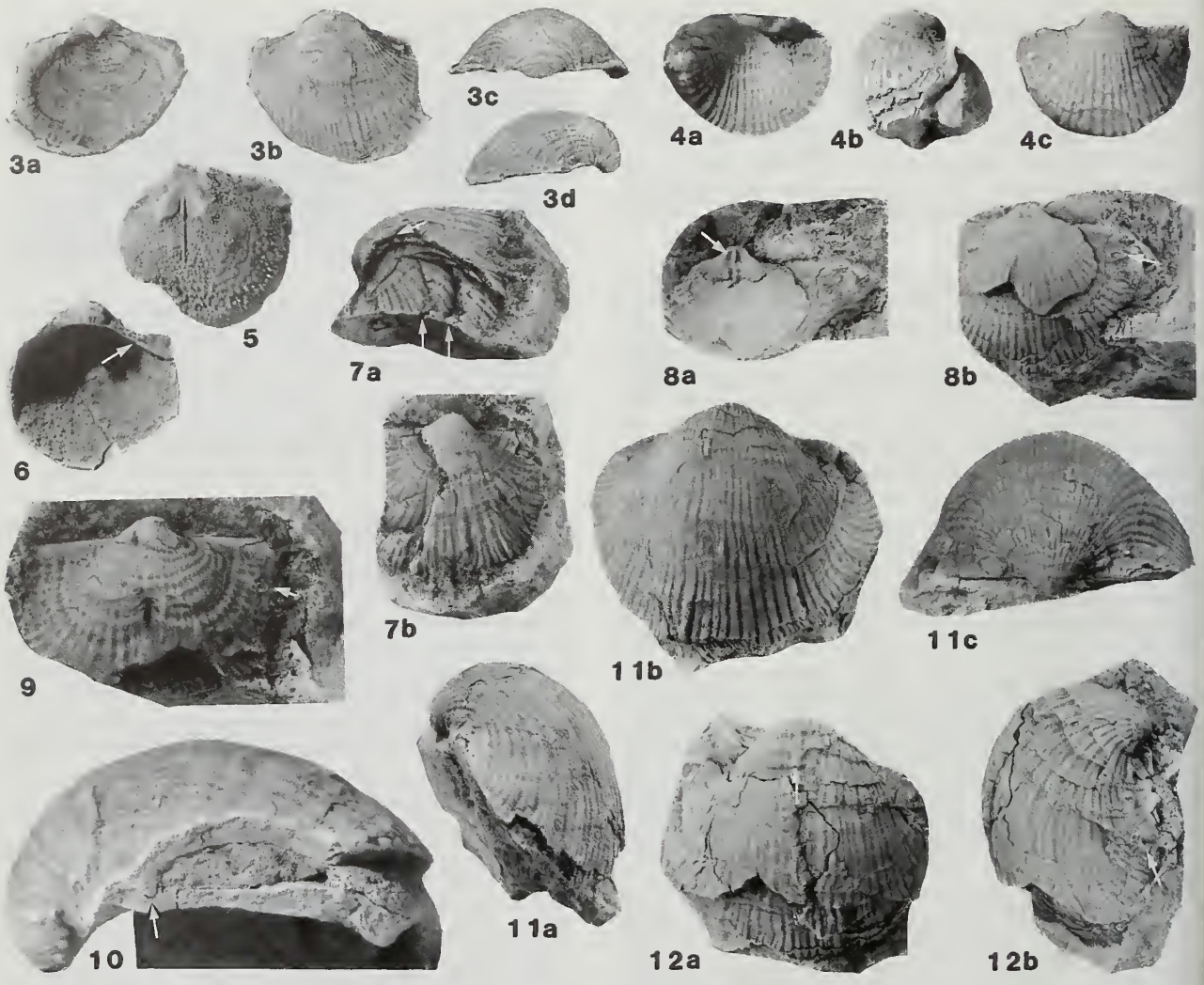


Figs 1, 2 *Productellina fremingtonensis* Reed, from the Pilton Beds of Fremington, north Devon, probably of lowest Tournaisian age. Specimens in the Sedgwick Museum, Cambridge. Fig. 1, latex mould of the dorsal valve exterior of the holotype described by Reed (1943) and figured by Whidborne (1898: pl. 22, fig. 2). E287, ×2. Fig. 2, internal mould of a ventral valve showing weak ribbing and the internal openings of paired spines (arrowed). H1665. x2.

Cambridge, reveals that this genus belongs in the Productininae. Its elongate outline, dorsal valve lamellae (Fig. 1), rather fine ventral ribbing and apparently single pair of flanking spines (Fig. 2) indicate an affinity with *Productina*. *Productellina* differs from *Devonoproductus* by apparently lacking spines over the entire ventral valve. As a member of the Productininae it is probably only slightly younger than *Dorsirugatia*. Thus we have an early division in this subfamily into two lineages of species; *Dorsirugatia* evolving into *Argentiproductus* while *Productellina* evolved into *Productina*.

In the mid Tournaisian of North America other elongate, weakly spinose and finely ribbed species evolved as *Productina sampsoni* Weller, 1909, and in late Tournaisian rocks *Productina parvula* Winchell, 1863 appears. The genus continued through the Viséan and, if the record of Winkler Prins (1968) of *P. pectinoides* (Phillips) is correct, the youngest record is from the early Bashkerian in north Spain.

The growth of long thin dorsal trails in this subfamily is characteristic. There is no evidence so far of ventral lamellae being as long, but we would not expect this. Dorsal valve growth involved no geniculation, but at all growth stages, after a length of a few mm, a short simple trail was composed of the margins of both valves. In order to accommodate the growing internal organs the geometry of the shell curvature necessitated periodical mantle regressions followed by rapid forward regrowth within (ventral to) the previous inner shell surface. In this way a series of long thin lamellose trails grew on dorsal valves. Each successive trail, although ventral to the last, allowed the new growth position to increase the depth of the body cavity slightly. Some of these lamellae grew to 10 mm or more in length, and as they became trapped in sediment they prevent easy extraction of dorsal valve exteriors. Thus dorsal valves are commonly found as exfoliated interiors. Although these dorsal trails grew as a consequence of shell geometry the survival advantage of this growth may have been two-fold. First, in the ability to maintain marginal trails during ontogeny which maintained a long narrow slit through which sea-water entering the mantle cavity could be monitored and 'filtered' (see Brunton, 1982, 1985); and secondly, in providing some protection to the dorsal valve against boring organisms. Brunton (1966) showed that in *Argentiproductus margaritaceus* only about half as many dorsal valves were bored as compared to ventral valves.



Figs 3–12 *Argentiproductus margaritaceus* (Phillips). Figs 3a–d, **neotype** (here selected), from Bishop's Quarry, Llandudno, north Wales, early Brigantian. Illustrated by Muir-Wood & Cooper (1960: pl. 123, figs 15, 16). Viewed dorsally, ventrally, posteriorly and laterally. BB13616.×1. Figs 4a–c, posterior, lateral and ventral views of a ventral valve exterior from near Mold, north Wales, showing characteristic ribbing and the paired flank spines. BB58627. ×1·5. Fig. 5, a dorsal valve interior from the same locality. BB58630. ×1·5. Fig. 6, a ventral valve interior from the same locality, showing the lateral ridge (arrowed). BB58629. ×2. Figs 7a–b, an incomplete shell with part of the ventral valve missing, showing the shallow body cavity (arrowed) and the lamellose nature of the dorsal valve exterior (arrowed). Stebden Hill. BD1643. ×1·5. Figs 8a–b, ventral valve exterior showing, at the exfoliated umbo, the internal mould of the ventral adductor muscle scars (arrowed), and the principal spine positions (arrowed). Stebden Hill. BD1645. ×1. Fig. 9, a ventral valve exterior showing growth deformation and spine bases (arrow); the shell damage results in a somewhat less inflated umbo than is typical for the species. This is a rare example from the framework facies. BD1634. ×1·5. Fig. 10, a shell from near Mold, north Wales, with one ear missing and showing the ventral lateral ridge fitting against the slight dorsal lateral ridge (arrowed). BB58628. ×5. Figs 11a–c, an example of the large form, viewed laterally, ventrally and posteriorly, from Parkhouse Hill, Derbyshire. B53583. ×1. Figs 12a, b, ventral and posterolateral views of a large specimen showing the somewhat lamellose nature of the valve surface and spine bases (arrowed). Caldbeck, Cumberland [Cumbria]. Natural History Museum (old collection) 75348. ×1.

Genus ***ARGENTIPRODUCTUS*** Cooper & Muir-Wood, 1951.

1928 *Thomasia* Fredericks: 790.
1931 *Thomasina* Paeckelmann: 181.
1942 *Thomasella* Paul: 191.
1951 *Argentiproductus* Cooper & Muir-Wood: 195.
1965 *Argentiproductus* Cooper & Muir-Wood; Muir-Wood: H471.
1966 *Productina* Sutton; Brunton: 208.

TYPE SPECIES. *Producta margaritacea* Phillips (1836: 215; pl. 8, fig. 8), by original designation of Cooper & Muir-Wood, 1951.

DIAGNOSIS EMENDED. Outline is hemispherical; profile is gently concavoconvex with short trails. Ribbing entire but variable, widening anteriorly. Lamellose, especially dorsally. Supporting spine rows extend from umbo across flanks,

spines rare anteromedially. Short lateral ridges in both valves.

DISCUSSION. The genus was placed in synonymy with *Productina* (Brunton, 1966) because the dorsal valve interiors of *Productina sampsoni,* figured by Muir-Wood & Cooper (1960: pl. 123, fig. 9) resembled extremely closely the dorsal interior of *A. margaritaceus*. The figure in Muir-Wood & Cooper (1960: pl. 123, fig. 17) purporting to be of *A. margaritaceus* is not of this species nor, we think, the genus; it may well belong to the linoproductids. The proliferation of more recently described species within the subfamily allows discrimination to be made between the two genera. *Argentiproductus* is commonly 20 to 25 mm wide across the body cavity (i.e. excluding ears). At a distance of 10 mm from the umbo about 6 to 10 ribs occur in 5 mm width; they are closely spaced, with flat to gently rounded crests. Because the ribs widen anteriorly and branch rarely, the number of ribs per unit width is variable. However, the ribbing on *Productina* species is finer, with rounded crests, and is more even over the entire shell. *Productina* is less wide but has a more strongly inflated ventral umbo giving steep flanks and a more strongly convex lateral profile than *Argentiproductus*. Spines are confined to ventral valves, but those on *Argentiproductus* are more prolific. Juvenile clasping spines (see Brunton, 1966) normally formed a ring just anterior to the initial point of pedicle attachment, the pedicle sheath, at about 0·5 mm from the tip of the umbo (Figs 13a, b). Thereafter a line of increasingly large support spines grew towards the anterior edges of the weakly defined ears, to a total of about six on each side. In addition the type species, and others in the genus, have one to three spines close to the mid-line, commonly only posteriorly, but rarely anteriorly also. Spines in *Productina* are confined to a few in each flanking row and are rare or lacking medially.

Argentiproductus margaritaceus (Phillips, 1836)
Figs 3–15

1836 *Producta margaritacea* Phillips: 215; pl. 8, fig. 8.
1861 *Productus margaritaceus* (Phillips); Davidson: 159; pl. 44, figs 5–7.
1960 *Argentiproductus margaritaceus* (Phillips); Muir-Wood & Cooper:182; pl. 123, figs 11–16.
1966 *Productina margaritacea* (Phillips); Brunton: 209; pl. 8, figs 1–19, pl. 15, figs 1–8.

DIAGNOSIS. *Argentiproductus* with well defined, but not strongly convex, ventral umbo and a concavoconvex profile with a shallow body cavity. Spines include one medially at about 10 mm from umbo. Dorsal and ventral adductor scars slightly raised.

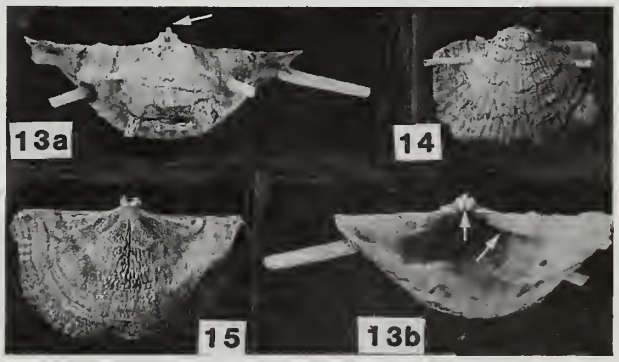
TYPE SPECIMEN. Neotype BMNH BB13616, here selected (Figs 3a–d), one of the specimens of *A. margaritaceus* (Phillips) selected by Muir-Wood to illustrate the genus and species in Muir-Wood & Cooper (1960); figure repeated in the brachiopod *Treatise* (1965). From the Bishop's Quarry Limestone, Bishop's Quarry, Llandudno, north Wales; the British Geological Survey Memoir (Warren *et al.* 1984) gives the age of this limestone as P_{1c}, early Brigantian. See Discussion, below.

MATERIAL. There are 64 specimens collected from the Craven Reef Belt by DJCM housed in the NHM and Liverpool Museum [NMGM]. Other specimens are from the Davidson and general collections at the NHM, including specimens from Bishop's Quarry, and the Sheffield City Museum. The large form is known from reef facies such as at Parkhouse Hill, Derbyshire and near Caldbeck, Cumbria. [The Caldbeck locality specimen in the NHM collections (75348) is recorded as from 'Falls Brew, Caldbeck', but we think this probably should be the locality Faulds Brow where quarries in high Viséan rocks were known. Both the specimen and its lithology indicate that reef facies are present in this area].

AGE. Late Asbian and early Brigantian, late Viséan.

DISCUSSION. Unlike most of the brachiopods described and figured by Phillips (1836) which were collected by William Gilbertson of Preston, this species was collected by Phillips himself while staying with Lord Cole (Sir P. Egerton) at Florence Court in County Fermanagh, Ireland, following the British Association meeting in Dublin of 1835. Although much of the Phillips collection is at the Oxford University Museum, examples of *A. margaritaceus* in that museum match neither the original Phillips illustration nor the refiguring of the specimen by Davidson (1861). An Oxford specimen, E2532, is undoubtedly conspecific, but is a representative of the larger form and about one-third larger than Phillips' illustrated specimen. The documentation with this specimen is sparse and there is some doubt as to whether it even originated from Phillips. For these reasons we have selected as neotype specimen one which well characterizes the common concept of the species and which the author of the genus herself selected to illustrate *Argentiproductus margaritaceus*. The neotype, when complete, would have been almost exactly the size of the Phillips specimen, as refigured by Davidson (1861), who pointed out that Phillips' illustration was somewhat enlarged.

A. margaritaceus is a variable species, especially in relation to its size and ribbing. The vast majority of specimens reach a maximun body width of about 25 mm, but a few rare specimens grew much larger, reaching about 40 mm across their visceral regions (Figs 11, 12). This gigantism is another example of the phenomenon discussed in *Antiquatonia* and



Figs 13–15 *Argentiproductus margaritaceus* (Phillips). Three silicified specimens from Asbian limestones near Derrygonnelly, Co. Fermanagh, Ireland. Figs 13a–b, posterior and anterodorsal views of a juvenile specimen showing the pedicle sheath (arrowed) and ventral lateral ridge (arrowed). Juvenile spines are well displayed. BB52916. ×6. Fig. 14, a ventral valve exterior showing the lamellose shell and spine positions. BB52907. ×2·3. Fig. 15, a young dorsal valve interior. BB52909. ×1·5.

Plicatifera by Timms & Brunton (1991), and is discussed further under *Plicatifera* herein (p.108).

The ribbing is characteristic in its anterior widening, rather flat-topped ribs and narrow interspaces. The density of ribs is very variable on any individual after a growth length of about 10 mm. The lamellose nature of the shell, especially of the dorsal valve, affected the height and dichotomy of ribbing. Rib dichotomy commonly occurred immediately posterior to a lamella, but anteriorly the two ribs commonly reverted to a single rib. As the shells grew so the rib width increased, by up to a factor, in adulthood, of about five times the early rib width (Fig. 4c). This expansion factor is even greater in the rare large specimens (Fig. 11b). The rib variability in association with lamellae and their variable increase in width results in inconsistent results of rib counts per unit width.

Internal morphology of the dorsal valve was described briefly by Muir-Wood & Cooper (1960) and of both valves by Brunton (1966). Noteworthy features are the lateral ridges in both valves diverging from the hinge lines (Figs 5, 6, 13b & 15). At early stages in ontogeny these ridges were built on earlier lines of prominent tubercules, and in adulthood they aided articulation, the ventral ridge fitting closely behind that of the dorsal valve (Fig. 10). Also in both valves the adductor muscle scars are raised and the internal surfaces of the valves, especially anteromedially, are strongly tuberculate. The dorsal median septum developed relatively late in ontogeny, never supported the cardinal process, but extends about 60% of the adult valve length. The cardinal process is sessile with a convex internal (ventral) surface from which the pair of grooved myophores converge dorsally in a V-shape.

The specimens described by Brunton (1966) as *P. margaritacea* are from rocks about 12 miles from Florence Court, the type locality, and both localities are considered as being of virtually the same Asbian age. These specimens are silicified and display external and internal morphology exceptionally well (see Figs 13–15); we believe that they represent the species, and thus the genus, particularly well.

The species is not common but occurs in western Europe more frequently in association with 'reefal' facies. Brunton (1985), based on initial work by Mundy (1980), described its distribution and that of *A. atripoides* (Gladchenko) on Stebden Hill, North Yorkshire. *A. margaritacea* is recorded in Europe, such as from the Viséan of Belgium (de Koninck 1847), the Brigantian of Poland (Zakowa 1985) and from the early Namurian of Kirghizia (Galitskaya 1977). It occurs also in the early Namurian of the Algerian Sahara (Pareyn 1962) and from mid Viséan rocks of northwest Australia (Roberts 1971).

Argentiproductus atripoides (Gladchenko, 1955)

Figs 16–21

1939 *Productus (Thomasina* ?) *atrypoides* Rotaï : 470 [466] (nomen nudum).
1955 *Productus (Thomasella) atripoides* Rotaï, 1937 (in litt.); Gladchenko: 13; pl. 1, figs 1–3.
1960 *Productus (Thomasella) atripoides* Rotaï, 1937 (in litt.); Gladchenko: 55; pl. 1, figs 1–3.
1977 *Productina atrypoida* (Rotai, 1963); Galitskaya: 27; pl. 5, figs 5–10; pl. 6, figs 9, 12.
1983 *Productina* (?) *atrypoida* (Rotay, 1939); Aizenverg: 77; pl. 41, figs 7, 8.
1985 *Productina* sp. undet., Mundy & Brunton: pl. 1, fig. 5.

DIAGNOSIS. Large *Argentiproductus,* rounded in outline, with almost flat valves (giving a very shallow body cavity), commonly distorted by hard substrate.

TYPE SPECIMEN. Lectotype, selected Aizenverg (1983), in the Leningrad (St Petersburg) Museum of F. N. Tchernyschew, collection N 5533, specimen 33; from Starobeshevo, Donbass, Upper Serpukhovian D_1 limestone = Arnsbergian.

MATERIAL. There are 31 specimens from the DJCM collection from Stebden Hill and one specimen from Elbolton (25 in the NHM and 7 in the Liverpool Museum). There are two specimens in the general collections of the NHM, one from Glutton, near Longnor, Derbyshire and the other from Treak Cliff, Derbyshire; all appear to be from reef framework facies. A single NHM specimen (B18021) of probable late Viséan age from Visé, Belgium.

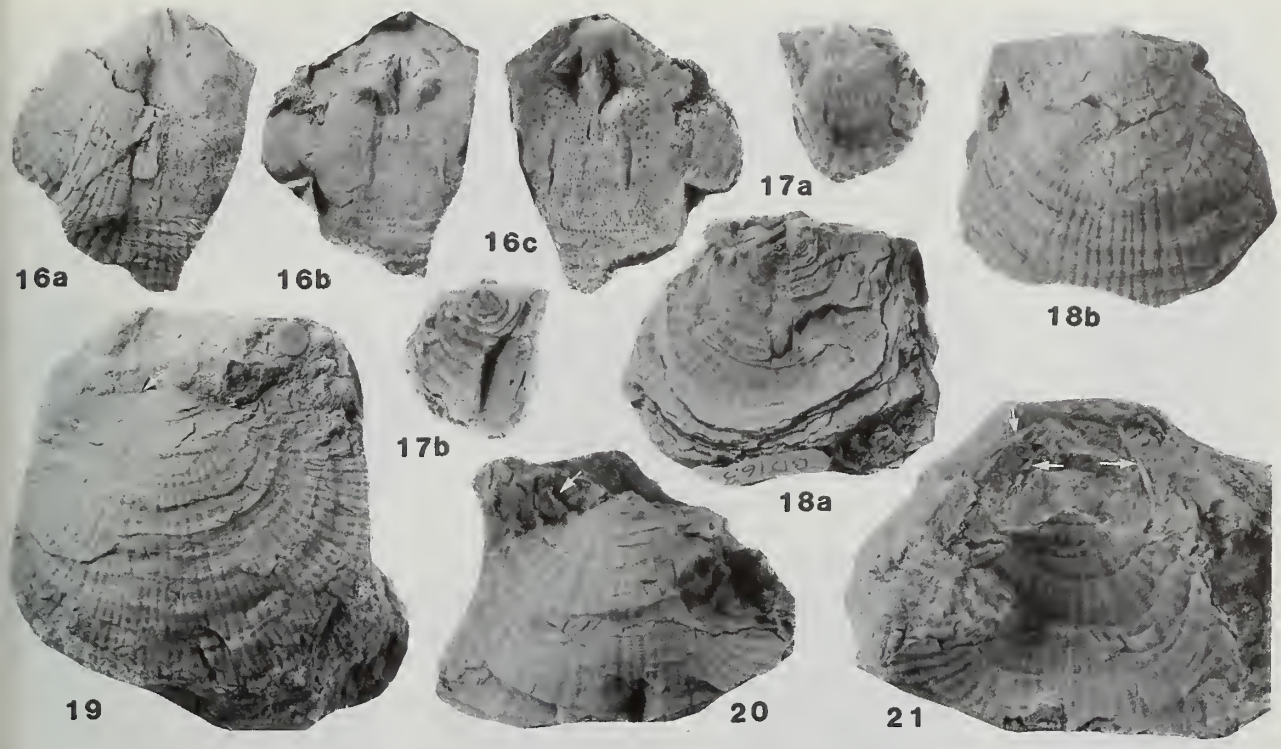
AGE. Late Asbian, in Britain, to early Namurian in the CIS (former USSR).

DESCRIPTION. The outline is subcircular, but retaining a straight hinge line with a maximum width of about 50 mm; it varied somewhat, depending on the degree of growth distortion. The ventral valve umbo may or may not extend beyond the hinge line. The lateral profile is commonly planoconvex, but with a minimum of ventral convexity leading to a very shallow body cavity. The curved length hardly exceeds the straight length. Concentric irregular rugae associated with lamellae are prominent on both valves. Ribbing has flattened crests and widens anteriorly, with six or seven ribs per 5 mm width at 10 mm from the umbo. Spines are distributed in a pair of rows from the umbo at an angle of about 20° from the hinge, with a maximum of seven to eight on each side (Fig. 19), many of which probably acted as clasping spines. Some specimens have rare additional body spines.

Internally the ventral valve resembles a very flat and broad *A. margaritaceus,* with elongate, slightly raised adductor scars. The very small ventral umbonal cavity means that the cardinal process is sessile. An alveolus may be present in some specimens, but a low and short median septum only arises between the anterior parts of the slightly raised adductor scars, which are ornamented dendritically. Weakly impressed brachial areas are irregularly surrounded by ridges, most prominently in the median sectors (Figs 16b, c). The valve surface is endospinose except posteromedially, behind the adductor scars. The ventral valve is also endospinose.

DISCUSSION. It has been common practice in Russia to attribute this species to Rotaï, at various dates. The earliest published mention of the species is Rotaï 1939: 470 [466], but he provided no description or illustration. We thus consider the first valid description to be that of Gladchenko (1955), which she repeated with the same illustrations in 1960. The lectotype was selected from Donbass material by Aizenverg in 1983. The age of this specimen, according to Poletaev *et al.* (1991), is early E_2 (=Arnsbergian).

The large size, style and width of ribbing and spines on the body anteromedially, although irregularly present because of attachment to hard surfaces, help to place the species in *Argentiproductus.* The large size and very flat form of the shell, with hardly any inflation at the tip of the ventral umbo, distinguish it from other species of the genus. All external characteristics, including the degree of ventral convexity, are variable because of the conditions under which the species



Figs 16–21 *Argentiproductus atripoides* (Gladchenko). Figs 16a–c, the largely exfoliated body cavity region of a specimen showing the ventral muscle scars and the mould of the dorsal interior, with (Fig. 16c) a latex cast of the dorsal valve interior. Stebden Hill. BD1620. ×1. Figs 17a, b, ventral and dorsal views of a juvenile specimen showing the early development of dorsal lamellae. Stebden Hill. BD1632. ×2. Figs 18a, b, dorsal and ventral views of a specimen showing the strong dorsal lamellae. Stebden Hill. BD1631. ×1·5. Fig. 19, ventral valve exterior showing lamellose shell and spine rows. Glutton, Derbyshire. B53582. ×1. Fig. 20, a ventral valve exterior with the row of flank spines on the left side (arrow) extending into the rock. Stebden Hill. BD1616. ×1·5. Fig. 21, posterodorsal view of an incomplete specimen showing the flanking spines (arrows) curving in a clasping fashion posteroventrally. Stebden Hill. BD1611. ×1·5.

lived, *viz*. within framework facies of Cracoean reefs in which other organisms provided local hard surfaces for attachment (see Brunton & Mundy 1988*b*, Mundy 1978, 1980). The extent to which ventral valves adpressed to hard sufaces or grew against hard objects influenced greatly the shape of the valve and its ornamentation. In addition specimens seem to have been prone to damage so that some shells display large areas of shell regeneration (Figs 18a, b). These characteristics make the species appear similar to the oyster-like bivalve *Pachypteria,* with which it is found in reef frameworks. No umbones are sufficiently well preserved to display the expected juvenile pedicle sheath, but at least some of the more median umbonal flanking spines were curved posteromedially, as if acting as claspers (Fig. 21). We have seen no indication of a cicatrix.

We attribute the Craven specimens to this species because of their close similarity to the species as illustrated by Gladchenko (1960) and Galitskaya (1977) from the Protvinsky horizon (=early Arnsbergian, Lower Namurian) of central Tien Shan, Kirkizia. Unfortunately details of the lithology from which the Tien Shan specimens came are unknown. Although the rocks of the Tien Shan are correlated with the Arnsbergian, some other species found at the same horizon indicate to us a slightly older age, nearer the base of the Namurian. Nevertheless, if the Craven specimens are correctly assigned it means that the species has a stratigraphical range of at least Asbian to within the Pendleian and early Arnsbergian.

Genus *PRODUCTINA* Sutton, 1938

1938 *Productina* Sutton: 151.
1965 *Productina* Sutton; Muir-Wood: H471.
1967 *Productina* Sutton; Carter: 289.

TYPE SPECIES. *Productus sampsoni* Weller (1909: 300; pl. 12, figs 18–22), by original designation of Sutton, 1938.

DIAGNOSIS. Slightly elongate outline, with an inflated umbo; ribbing distinct and regular with rounded crests. Spines few at flanks and may be lacking medially.

DISCUSSION. *Productina* species differ from the late Devonian genus *Dorsirugatia* (Lazarev, 1992 & herein, p.117) in having a more inflated ventral umbo and well defined regular ribbing. *Productina* differs from *Argentiproductus* in being more elongate in outline, and more globose in profile (i.e. with an inflated ventral umbo), with a less lamellose ventral valve (retaining a strongly lamellose dorsal valve); in consequence the ribbing is more regular. The ribs are rounded in section and, while they widen anteriorly, this feature is less marked than in *Argentiproductus*. The posterolateral spine patterns are similar in both genera, but *Productina* tends to lack or to have very few median spines. A feature common to both genera is the tendency for rib branching to occur in association with lamellae. In the more strongly ventrally lamellose *Argentiproductus* species this results in a varied ribbing, both in terms of rib width and degree of development

of the ribs. Quite commonly, immediately anterior to a lamella the ribbing diminishes or reverts to a low single rib where posteriorly it had divided. On the less lamellose *Productina* species the ribbing is more continuous, less varied in dimensions and each rib has a more rounded crest.

Internally the two genera are more similar than indicated by Muir-Wood & Cooper (1960: 182) because of their use of a misidentified dorsal interior (1960: pl. 123, fig. 17), belonging perhaps to a linoproductid species. However, even with incomplete knowledge of interiors of all species, it seems that some congeneric species display as much variation as is seen between the two type species.

Sutton's genus is based on *P. sampsoni* from the Chouteau Limestone of Missouri, of upper Kinderhookian age (= Hastarian, Lower Tournaisian). In North America *P. parvula* (Winchell, 1863), from similarly aged rocks in Iowa, and possibly *P. lodgepolensis* Rodriguez & Gutschick (1968), from mid Tournaisian rocks of Montana, belong to this genus. Roberts (1963, 1976) described several Tournaisian to Viséan species from Australia, but following Brunton (1966) assigned them to *Productina*. We assign his *P. macdonaldi* to *Argentiproductus* but keep his *P. globosa*, of late Tournaisian age, and *P. striata*, of mid Viséan age, in *Productina*. Of Paeckelmann's (1931) two species from Germany, *P. decheni* of Tournaisian age probably belongs here, but *P. transveristriatus* cannot be assigned with confidence. In Britain we assign *P. pectinoides* Phillips (1836) to *Productina* and compare some species from the Craven Reef Belt to the species. Winkler Prins (1968) and Martinez Chacon (1979) recorded poorly preserved material as *P. pectinoides* from early Bashkerian strata. The genus, therefore, extends from the early Tournaisian to rocks of early Bashkerian age.

Productina pectinoides (Phillips, 1836) Figs 22, 23

1836 *Producta pectinoides* Phillips: 215; pl. 7, fig. 11?
?1931 *Productus (Thomasina) pectinoides* (Phillips); Paeckelmann: 188; pl. 17, figs 13, ?14–16.
?1968 *Productina pectinoides* (Phillips); Winkler Prins: 75; pl. 1, figs 13, 14.
?1979 *Productina pectinoides* (Phillips); Martinez Chacon: 132; pl. 12, figs 14–23.
1985 *Productina pectinoides* (Phillips); Zakowa: 308; pl. 3, figs 1–6.

DIAGNOSIS. Large for genus, reaching about 30 mm wide, with small ears almost forming maximum shell width. Ventral valve with weak lamellae; ribs regular, with rounded crests, approximately 10 per 5 mm width at 10 mm from umbo.

TYPE SPECIMEN. Lectotype, here chosen, BMNH B8947 (Figs 22a–c) in the Gilbertson Collection and figured by Phillips (1836: pl. 7, fig. 11). The locality is given as 'Bolland'.

MATERIAL. A second smaller specimen (paralectotype) in the Gilbertson Collection, BMNH BB65110; about 12 other NHM specimens including material from the reefal facies at Narrowdale (e.g. B48709–18), Staffordshire. One specimen from Kendal, Cumbria, in the Sedgwick Museum, Cambridge (E9710).

AGE. Chadian to Asbian, and possibly Brigantian.

DISCUSSION. It is a common feature of specimens described by Phillips that details of their localities are unknown. Thus this species is recorded as 'Bolland', a region extending northeast of Preston and to the northwest of Clitheroe, roughly centred on the river Hodder and now forming part of the area known as the Forest of Bowland, Lancashire. Thus precise localities and ages remain unknown. However, it seems that true examples of the species occur in the Clitheroe area in Chadian rocks belonging to the Clitheroe Limestone Formation of Riley (1990*b*), who demonstrated that the Chadian in this area lies within the late Tournaisian. The Phillips specimens could also be of this age.

Productina specimens from the Craven faunas were initially identified by us as *P. praemargaritaceus* (Sergunkova), and this name was used by Brunton & Tilsley (1991) for some specimens from Treak Cliff, Derbyshire. *P. praemargaritaceus* is a Russian Tournaisian species and we now recognize that it differs from the Craven Reef Belt specimens, and others identified here as *P. pectinoides*, by being wider and less globose, so we assign it to *Argentiproductus*. The Treak Cliff specimens referred to above should be called *P.* cf. *pectinoides*. The Craven Reef Belt specimens collected by Mundy are rare and not all are well preserved. While one is a good match to the small Gilbertson specimen of *P. pectinoides* the others belong less clearly to the species. Thus in order to retain a clear diagnosis of *P. pectinoides* we separate the Craven specimens below as *P.* cf. *pectinoides*.

The large forms of *A. margaritaceus* somewhat resemble large examples of *P. pectinoides*, but the ribbing, ventral lamellae and more spinose *Argentiproductus* species distinguish them. *P. pectinoides* has a more strongly inflated umbonal region than *Argentiproductus* species and its more evenly ribbed and less lamellose shell produces a more regular appearance. In addition, in this species the angle at which spines diverge from the hinge line is less, at about 10°, than the *c.* 15°–20° in *Argentiproductus*.

The species name has not been used much in European literature. Those specimens described by Paeckelmann (1931), Winkler Prins (1968) and Martinez Chacon (1979) may not be entirely conspecific, while the late Asbian and Brigantian record of Zakowa (1985) looks accurate.

Productina cf. *pectinoides* (Phillips, 1836) Figs 24–28

MATERIAL. Twelve specimens in the DJCM collection largely from Butter Haw Hill, and a single specimen from the same locality in the Liverpool Museum.

AGE. Asbian.

DISCUSSION. We compare this material to *P. pectinoides* since its preservation is imperfect and we cannot be fully confident that it is conspecific with Phillips' species. These specimens are found contemporaneously with *A. margaritaceus* in the Craven Reef Belt, but differ by the generic characters already discussed. The specimens are all small, reaching a maximum width, just anterior of the ears, of 14 mm. While they resemble the lectotype of the species in most aspects, the degree of umbonal convexity (inflation) is slightly less and three specimens have ribs which anteriorly became wider, and thus resemble *A. margaritaceus*. We have separated the Craven specimens here from the true *pectinoides* so as to present a 'clean' diagnosis of the species.

In the final section of this paper (p.116) we discuss the stratigraphical relationships of this species with others of the subfamily.

Figs 22–23 *Productina pectinoides* (Phillips), from the Gilbertson Collection, figured by Phillips (1836), Bolland, Lancashire. Figs 22a–c, the **lectotype** (here selected), viewed laterally, ventrally and posteriorly. B8947. ×1. Figs 23a–c, the second small specimen (paralectotype) in the Gilbertson Collection, viewed ventrally, laterally and posteriorly. BB65110. ×1.

Figs 24–28 *Productina* cf. *pectinoides* (Phillips). Figs 24a, b, a small specimen in lateral and ventral views. Skelterton Hill. BD1674. ×2. Figs 25a, b, oblique anterolateral and ventral views of an incomplete specimen, showing the shallow body cavity (arrowed). Butter Haw Hill. BD1667. ×2. Fig. 26, a ventral view, showing one spine (arrowed). Butter Haw Hill. BD1668. ×1·5. Figs 27a, b, ventral and lateral views of a specimen with one pair of flank spines (arrowed) near the ears. Butter Haw Hill. BD1666. ×2. Figs 28a, b, lateral and ventral views of a large specimen from the Kendal area, Cumbria, closely resembling the type specimen. Sedgwick Museum, Cambridge, E9710. ×1.

Family **PLICATIFERIDAE** Muir-Wood & Cooper, 1960

DIAGNOSIS EMENDED. Small to medium productoids in which the ventral visceral disc is only gently convex, giving a shallow to moderate body cavity. Concentric ornament is strong, the ribbing weak to lacking. Spines commonly confined to ventral valves. Internal dorsal marginal structures are usual.

Subfamily **PLICATIFERINAE** Muir-Wood & Cooper, 1960

DIAGNOSIS EMENDED. Plicatiferids with moderately deep body cavities, strongly rugose or lamellose visceral discs and dorsal ear baffles.

DISCUSSION. These familial diagnoses differ from those given in 1960 or the *Treatise* (1965) as they are new working diagnoses for the revision of the brachiopod *Treatise* now in progress. Muir-Wood & Cooper's (1960) subfamily included only *Plicatifera*. The newly evolving classification elevates the taxon to family level with the inclusion of several subfamilies and many more genera.

The Plicatiferidae includes genera from late Devonian to early Permian, while the subfamily is confined to Viséan and Namuriam rocks, the genera from western Europe being *Plicatifera, Aseptella* Martinez Chacon & Winkler Prins (Namurian of north Spain) and the new genus *Admodorugosus* described herein (p.111).

Genus ***PLICATIFERA*** Chao, 1927

1927 *Plicatifera* Chao: 25
1960 *Plicatifera* Chao; Muir-Wood & Cooper: 201
1965 *Plicatifera* Chao; Muir-Wood: H476
1966 *Plicatifera* Chao; Brunton: 203

TYPE SPECIES. *Productus plicatilis* J. de C. Sowerby, 1824, by original designation of Chao, 1927.

DIAGNOSIS. Plicatiferinae with strong posterior rugae and variably developed ribbing, producing posterior reticulation in some species. Trails are smooth or faintly ribbed. Few spines are confined to ventral valves. The body cavity becomes deep anteriorly and ear baffles are prominent.

DISCUSSION. *Plicatifera* is a characteristic and well-recognized genus in the Upper Viséan of Europe and parts of Asia. In profile the rugose visceral regions are rather flat,

with the strongest convexity occurring with the anteriormost rugae and start of the trail, which can be long. The dorsal valve of adult shells curves strongly (geniculates) against the ventral valve trail. Brunton (1966) commented upon the considerable size differences amongst specimens in the Sowerby type collection and suggested that further work might show that the larger forms should be named differently. Initially our study of specimens, showing similar size variation, inclined us to separate as new species the specimens about twice the size of those more commonly found, including the type specimens of both *P. plicatilis* and *P. pseudoplicatilis* Muir-Wood. However, as more specimens were studied the separation of these two groups narrowed and work first carried out by Timms (1978) indicated that these variations might be growth phenomena. Timms & Brunton (1991) pursued the idea and demonstrated that possibly *Plicatifera* specimens reached varied sizes by the time they geniculated, according to whether they grew rapidly or relatively slowly, and the length of time over which they grew before the geniculation event, which they equated with sexual maturity.

Plicatifera plicatilis (J. de C. Sowerby, 1824)

Figs 29–35

1824 *Producta plicatilis* J. de C. Sowerby: 85; pl. 459, fig. 2.
1914 *Pustula plicatilis* (J. de C. Sowerby); Thomas: 331; pl. 20, fig. 22.
1927 *Plicatifera plicatilis* (J. de C. Sowerby); Chao: 25.
1930 *Plicatifera plicatilis* (J. de C. Sowerby); Muir-Wood: 107.
1960 *Plicatifera plicatilis* (J. de C. Sowerby); Muir-Wood & Cooper: 201; pl. 56, figs 13–21 (?*non* figs 22, 23).
1965 *Plicatifera plicatilis* (J. de C. Sowerby); Muir-Wood: H477.
non 1966 *Plicatifera plicatilis* (J. de C. Sowerby); Brunton: 204; pl. 6, figs 6–15; pl. 7, figs 1–18.
1985 *Plicatifera plicatilis* (J. de C. Sowerby); Zakowa: 304; pl. 1, figs 5–7, pl. 2. figs 1–3.

DIAGNOSIS. *Plicatifera* lacking ribbing on visceral discs and trails.

TYPE SPECIMEN. Lectotype, BMNH B60960 (Figs 29a–c), designated by Thomas (1914: 331) when numbered 43392, from the Sowerby Collection. Locality unknown, other than Derbyshire.

Figs 29–35 *Plicatifera plicatilis* (J. de C. Sowerby). Figs 29a–c, the lectotype viewed anteroventrally, posteriorly and dorsally. Derbyshire. B60960. ×2. Figs 30a–c, posterior, lateral and anterior views of a specimen showing the smooth trail, spine bases and well developed median ventral sulcus. Elbolton. BD1602. ×1·5. Fig. 31, an incomplete specimen viewed anteriorly showing the gentle convexity of the visceral disc and smooth trail. Stebden Hill. BD1569. ×1·5. Fig. 32, a dorsal and a ventral valve, the latter showing two major spines from the anterior (arrowed). Derbyshire. B2471. ×1. Figs 33a, b, ventral and dorsal views of a specimen lacking its ears and most of the trail. Stebden Hill. BD1604. ×1. Figs 34a, b, a large example viewed ventrally (×1) and ventrolaterally (×1·5), showing some of the spine bases. Elbolton. BD1597. Figs 35a–c, dorsal, ventral and posterior views of one of the two larger specimens from the Sowerby Collection. Ventral spine bases and corresponding dorsal dimples can be seen. Derbyshire. B60962. ×1.

MATERIAL. Two other large specimens from the Sowerby Collection and numerous other specimens in the NHM; the DJCM collection contains 112 specimens in the NHM, from Stebden Hill and Elbolton, while 21 specimens from the same area are in the Liverpool Museum collections. Other specimens at the British Geological Survey, Keyworth, from Derbyshire and Yorkshire; the Sedgwick Museum, Cambridge, from Settle, Yorkshire; and in the Sheffield City Museum from near the Derbyshire/Staffordshire borders.

AGE. The Mundy collection specimens are all of Asbian, B_2 age, and the localities of other specimens, where sufficiently well known, indicate an Asbian age, late Viséan.

DISCUSSION. Two similar species of *Plicatifera* occur in the British Asbian, the type species and *P. pseudoplicatilis* Muir-Wood, 1928, described below. In 1966 Brunton incorrectly thought that the two were conspecific, so his very full description of '*P. plicatilis*' turns out to be what we would now call *P. pseudoplicatilis*, principally recognized by its ribbing and consequently reticulate visceral areas. Interiors of the two species seem to be very similar.

A variable feature of the Craven Reef Belt collections, but seen also in specimens from elsewhere, is a sulcation of the ventral valve which causes a posterior flexure in the anterior outline of the rugose area medially (Figs 30a, 32). Out of 46 well-preserved specimens of *Plicatifera plicatilis* in the NHM and Liverpool collections, 27 (59%) are sulcate; out of 44 good specimens of *P. pseudoplicatilis* 9 (20%) are sulcate. It is notewothy that the non-sulcate specimens almost always include the rare large examples referred to above. The curved lengths measured to the last ruga of geniculated specimens range from *c.* 12 mm to *c.* 35 mm. The body width (i.e. maximum width other than at the ears) is about 25 mm in the normal-sized specimens and about 44 mm in the large specimens.

Plicatifera pseudoplicatilis (Muir-Wood, 1928) Figs 36–46

1928 *Productus pseudoplicatilis* Muir-Wood: 189; pl. 11, figs 17a–c.
1930 *Eomarginifera pseudoplicatilis* (Muir-Wood); Muir-Wood: 204.
1966 *Plicatifera plicatilis* (J. de C. Sowerby); Brunton: 203; pl. 6, figs 6–15; pl. 7, figs 1–8.

DIAGNOSIS. *Plicatifera* with ribbing starting close to umbones and extending onto trails. Visceral discs are reticulate, but commonly non-sulcate.

TYPE SPECIMEN. Holotype, BMNH B20540 (Figs 36a–c) from Settle, Yorkshire (Muir-Wood 1928: 190).

MATERIAL. The NHM collections include 43 good specimens in the DJCM collection from Butter Haw and Stebden hills, and 11 more from the same localities are in the Liverpool Museum; there are several of the normal-sized specimens and one large specimen in the Sheffield City Museum.

AGE. Specimens from the Craven Reef Belt are all Asbian, B_2, and no other studied specimen contradicts this age.

DISCUSSION. The species was fully described from finely silicified material by Brunton (1966) (Figs 43–46), but then named *plicatilis*. The species is closely similar to *plicatilis*, differing mainly in that after a length of about 5 mm ribs started to grow which persisted until well beyond the last ruga and onto the trail (Fig. 39). This produced a reticulation on both valves in the rugose regions, but the rugae always predominate. Another difference is the dominance in *pseudoplicatilis* of non-sulcate specimens, which thus have a more regularly rounded anterior outline to the visceral region (Figs 36c, 40b).

As in *P. plicatilis* this species also has a rare large form, figured here from the reef facies of Narrowdale, Staffordshire (Figs 42a–d). Dimensions of the normal small and large forms of *pseudoplicatilis* specimens are a few mm less than those of *plicatilis*.

Subfamily **LEVITUSIINAE** Muir-Wood & Cooper, 1960

DIAGNOSIS, EMENDED. Plicatiferids with long trails and moderate to deep body cavities. Ribbing is lacking; rugae may be weak and marginal structures are lacking.

Genus ***ACANTHOPLECTA*** Muir-Wood & Cooper, 1960.

TYPE SPECIES. *Producta mesoloba* Phillips (1836: 215; pl. 7, figs 12, 13) by original designation of Muir-Wood & Cooper (1960).

DIAGNOSIS. Moderate sized shells with weak irregular rugae posteriorly. A median dorsal narrow sulcus and ventral fold bearing spines extends from disc to trail, the latter having small marginal flares or gutters.

COMMENT. The genus has been recorded in North America, north Africa, western Europe, Poland and Russia. It is not recorded with any confidence from the eastern C.I.S., China or Australia.

Acanthoplecta mesoloba (Phillips, 1836) Figs 47–53

1836 *Producta mesoloba* Phillips: 215; pl. 7, figs 12, 13.
1861 *Productus mesolobus* (Phillips); Davidson: 178; pl. 31, figs 6–9.
1914 *Pustula mesoloba* (Phillips); Thomas: 327; pl. 20, figs 18–21.
1930 *Plicatifera mesoloba* (Phillips); Muir-Wood: 107.
1960 *Acanthoplecta mesoloba* (Phillips); Muir-Wood & Cooper: 171; pl. 44, figs 10–17.
1966 *Acanthoplecta mesoloba* (Phillips); Brunton: 201; pl. 5, figs 16–22; pl. 6, figs 1–5.

DIAGNOSIS. Strongly and evenly concavoconvex in profile, with moderate body cavity. Ventral median fold in shallow sulcus, with spines, corresponding to dorsal weak sulcus. Adult trails with narrow anterolateral gutters.

TYPE SPECIMEN. Lectotype here chosen, Phillips' specimen figured on his plate 7, figure 12, BMNH B427, from Bolland (Figs 52a–b). Thomas (1914) misleadingly reported the types as lost, but the original specimens for Phillips' figures 12 and 13 are preserved in the Gilbertson Collection, used extensively by Phillips for his illustrations in 1836. The lectotype retains the original Gilbertson register number 160, proving that it came from the Bolland area rather than Derbyshire, the second locality mentioned by Phillips (1836: 215).

MATERIAL. Of the DJCM collections there are 33 specimens in the Liverpool Museum and 27 in the NHM. The latter

Figs 36–42 *Plicatifera pseudoplicatilis* (Muir-Wood). Figs 36a–c, the holotype of Muir-Wood (1928) in dorsal, lateral and posterior views. The shell material is partially missing, especially from the ventral valve, so that ribbing is less distinct. Settle, Yorkshire. B20540. ×1·5. Figs 37a, b, ventrolateral and posterior views of a slightly exfoliated specimen. Stoney Middleton, Derbyshire. Sheffield City Museum H88–196. ×1·5. Figs 38a, b, ventral and dorsal views. Stebden Hill. BD1565. ×1·5. Fig. 39, anterolateral view of a specimen showing the ribbing on the trail. Butter Haw Hill. BD1553. ×1·5. Figs 40a, b, dorsal and ventral views of an incomplete specimen. Butter Haw Hill. BD1584. ×1·5. Fig. 41, an exfoliated dorsal valve interior. Stebden Hill. BD1562. ×1·5. Figs 42a–d, lateral, posterior, ventral and dorsal views of a large specimen showing the ribbing extending onto the trail and spine bases on the ventral and lateral surfaces. Narrowdale, Staffordshire. B45692. ×1·5.

collections also contain about 40 other specimens from Staffordshire, Derbyshire, Yorkshire, Ireland, North Wales, the Midland Valley of Scotland, and the Isle of Man. There are a few specimens, some cited by Thomas (1914), in the British Geological Survey collections and about 15, mostly from Derbyshire, in the Sheffield City Museum.

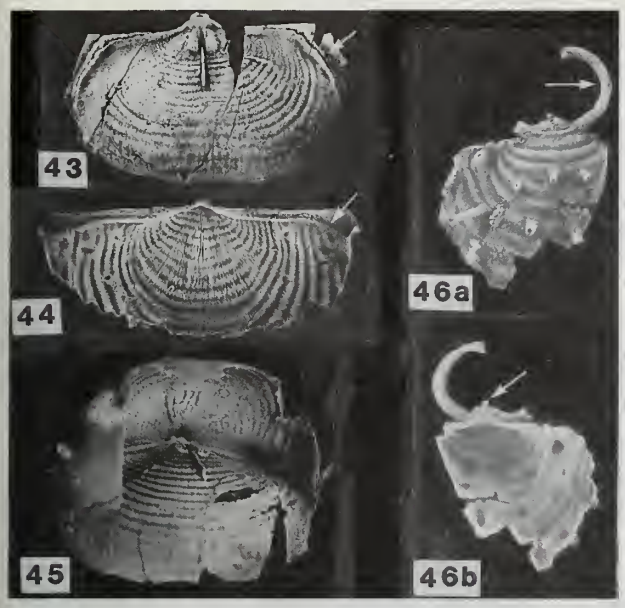
AGE. Most of the above specimens are thought to be of upper Viséan, Asbian to early Brigantian age. However, there are a few specimens named *A. mesoloba* in the NHM collections from Thorpe Cloud, Derbyshire, generally considered as of Chadian age, and Thomas (1914) referred to a specimen which may be of Arundian age. The species has been recorded from Brigantian (P_2) reef facies of the Eyam Limestone Formation near Monyash, Derbyshire by Gutteridge (1990). We thus attribute an age of Chadian to Brigantian for the species. The relationship of these Chadian rocks to the Tournaisian/Viséan boundary in this area is unclear.

DISCUSSION. While the species occurs most commonly during Asbian times it also occurs in Chadian and Brigantian reef facies. The Chadian records from Thorpe Cloud are specimens possibly displaying some differences as compared to the types, such as a more regular rugation and less well defined median fold and sulcus; the spine bases also seem less prominent. In the Sedgwick Museum, Cambridge, there are four (E9745–48) small specimens from County Clare, Ireland, only about 18 mm wide and somewhat resembling the Thorpe Cloud material; these may also therefore be early Viséan in age.

The NHM specimens, including those from the Craven Reef Belt, display a range in adult size comparable to the range discussed above for *Plicatifera*. There is also variation in the strength of development of the median sulcus within which lies the narrow ventral fold. Commonly these structures make little difference to the general anterior outline, but in some specimens the depth of the sulcus causes an emargination anteriorly. Again this feature is comparable to the more sulcate forms of *P. plicatilis*.

The species is a rare constituent of the fauna from County Fermanagh described by Brunton (1966), but a full description was given, including illustrations of the dorsal valve gutter bordering the trail (Figs 49a–c). This stucture tends to have been lost from specimens cracked out from the rock, but the lectotype, and a few others, show the start of the outward curve of the trail (Fig. 52a) which, if complete, would have been the gutter.

The species differs from *Plicatifera* in being more regularly convex, with no true geniculation in either valve. This convexity of the dorsal valve produced a body cavity shallower than in adult *Plicatifera,* and the outline is also more rounded. The low irregular rugae, double row of spines close to the hinge line and median fold and sulcus further distinguish this species from *Plicatifera. A. mesoloba* differs from *Admodorugosus* (below) by being at least twice as wide across the body, in its non-rugose and guttered trail, and median fold and sulcus.



Figs 43–46 *Plicatifera pseudoplicatilis* (Muir-Wood). Four silicified specimens from the Asbian of Co. Fermanagh, Ireland. Fig. 43, a dorsal valve interior showing the lateral ridges and ear baffles (arrowed), adductor scars and faint brachial ridges. BB52835. ×1·7. Fig. 44, an incomplete ventral valve interior showing lateral ridges (arrowed), adductor and diductor muscle fields. BB52834. ×2. Fig. 45, incomplete articulated dorsal and ventral valves showing the deep adult body cavity and the way in which the lateral ridges fit together. BB52837. ×1·7. Figs 46a, b, a juvenile ventral valve viewed externally and internally, showing the initial clasping spines (arrowed), other juvenile spines and the pedicle sheath (arrowed). BB52840. ×10.

A. mesoloba occurs in western Europe, Poland and Russia (Moscow basin).

Genus *ADMODORUGOSUS* nov.

DIAGNOSIS. Small to medium sized plicatiferinid with prominent concentric rugation covering both valves, but lacking radial ornament. Few scattered spines are confined to ventral valves. Body cavity is moderately shallow.

NAME. Latin, *admodum* = entirely, *rugosus* = wrinkled.

TYPE SPECIES. *Admodorugosus cracoensis* nov.

DISCUSSION. Only the type species is recognized, and it is described below.

Admodorugosus has been confused in the past most commonly with *Acanthoplecta* Muir-Wood & Cooper or *Plicatifera* Chao. When complete specimens are available those genera are differentiated by their smooth trails, the posterior ribbing of some *Plicatifera* species and the median spine-bearing ridge, within a sulcus, on *Acanthoplecta*. If only the posterior, visceral regions are available identification is less easy, but *Admodorugosus* is more rounded in both profile and outline than the other two genera. The rugation of the new genus is more comparable to that of *Plicatifera* than to that of *Acanthoplecta*, but adult *Plicatifera* specimens of the more common smaller dimensions may reach about twice the width of adult *A. cracoensis*, and their outlines are more quadrate. *P. pseudoplicatilis* (Muir-Wood) is also radially ornamented, producing a somewhat reticulate visceral region.

Other plicatiferid or leioproductid genera of different ages (and thus not expected in Viséan rocks) lack the clear rugation of *Admodorugosus*. The rugation on the Upper Devonian *Planoproductus* Stainbrook is weak and impersistent; in addition the ventral valve is covered by small spines. It should be classed with *Rugauris* Muir-Wood & Cooper in a separate family group. The leioproductid *Magnumbonella* Carter, from the Tournaisian of the U.S.A., has fine rugae posteriorly, but they do not extend onto the trails. Another rugose genus is *Acanthoproductus* Martynova from the late Famennian of Kazakhstan, but its rugae fail to extend onto the trail and posteriorly there are elongate spine bases which would seem to place the genus in the subfamily Semiproductinae McKellar 1970.

Admodorugosus cracoensis sp. nov. Figs 54–60

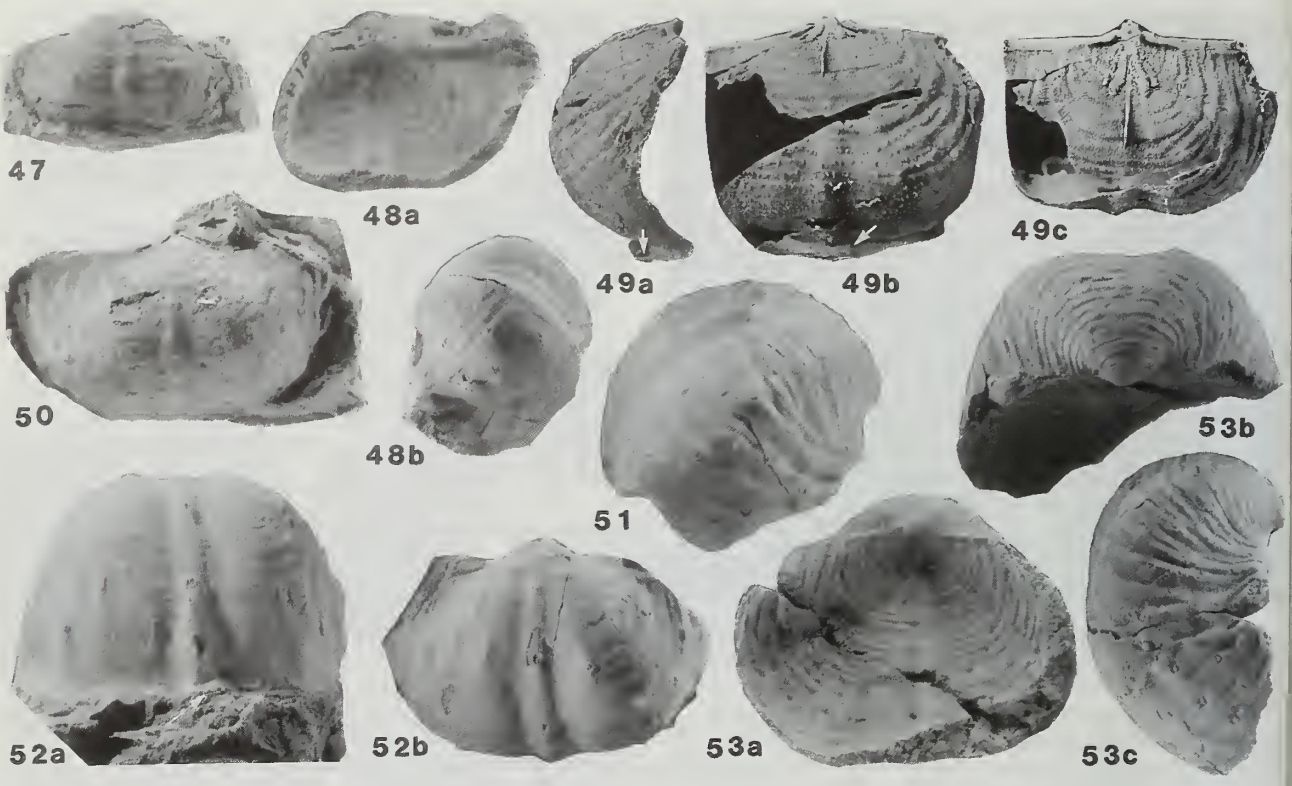
NAME. The species is named after the village of Cracoe, North Yorkshire, which also gives its name to the tract of reef limestones from which many of the known specimens were collected.

DIAGNOSIS. As for the genus.

LOCALITY AND HORIZON. The type locality is Butter Haw Hill (Grid Ref. SD 9964 6104), 11 miles (18 km) east of Settle, North Yorkshire, in late Asbian (B_{2b}), Dinantian reef limestones.

HOLOTYPE. Specimen in The Natural History Museum, London, BMNH, BD2447 (Figs 54a–d), from Butter Haw Hill, North Yorkshire, collected by DJCM.

MATERIAL. The 37 specimens (paratypes) examined in addition to the holotype are as follows: Eighteen specimens collected by DJCM from precise localities on Butter Haw Hill (BD2439–56, less BD2441–4,6), Skelterton Hill (BD2432–37), and Stebden Hill (BD2441–43), North Yorkshire. Five specimens from the 'Cracoe Reef Knolls' in the Garwood collection of the British Geological Survey, (67064–68); two Cracoe district specimens in the Liverpool Museum, (1976.249 Ex-Ey); two specimens from Treak Cliff, Castleton, Derbyshire, one in the Liverpool Museum collected by P.W. Phillips (1972.346.E), the other, collected by Dr P. Cossey, in the NHM (BD2446). Also in the Liverpool Museum are two possible specimens from Little Orme, north Wales. In the Sheffield City Museum there are four unnumbered Bateman collection specimens, possibly from Wetton, and one specimen (H88–244, called *mesolobus*) from Stoney Middleton, Derbyshire. The J.W. Jackson collection at Buxton contains a specimen (JWJ15112) from Peak Hill near Castleton and two from Narrowdale (JWJ15948). Other specimens, all in the NHM, are six collected by Carrington, in the Davidson Collection, from Wetton, Staffordshire (B5784, BD3206, BD3347–50); one Davidson Collection specimen from Narrowdale, Staffordshire (B13811); three specimens collected by Wheelton Hind from Narrowdale (B53674, B53677); three specimens in the Gilbertson Collection from Bolland (B429, B439, BD3202); one specimen collected by J.S. Turner from Little Island, Cork, Ireland (B95512); and one collected by P. Cambridge from Wirksworth Quarry, Derbyshire (BD6577).



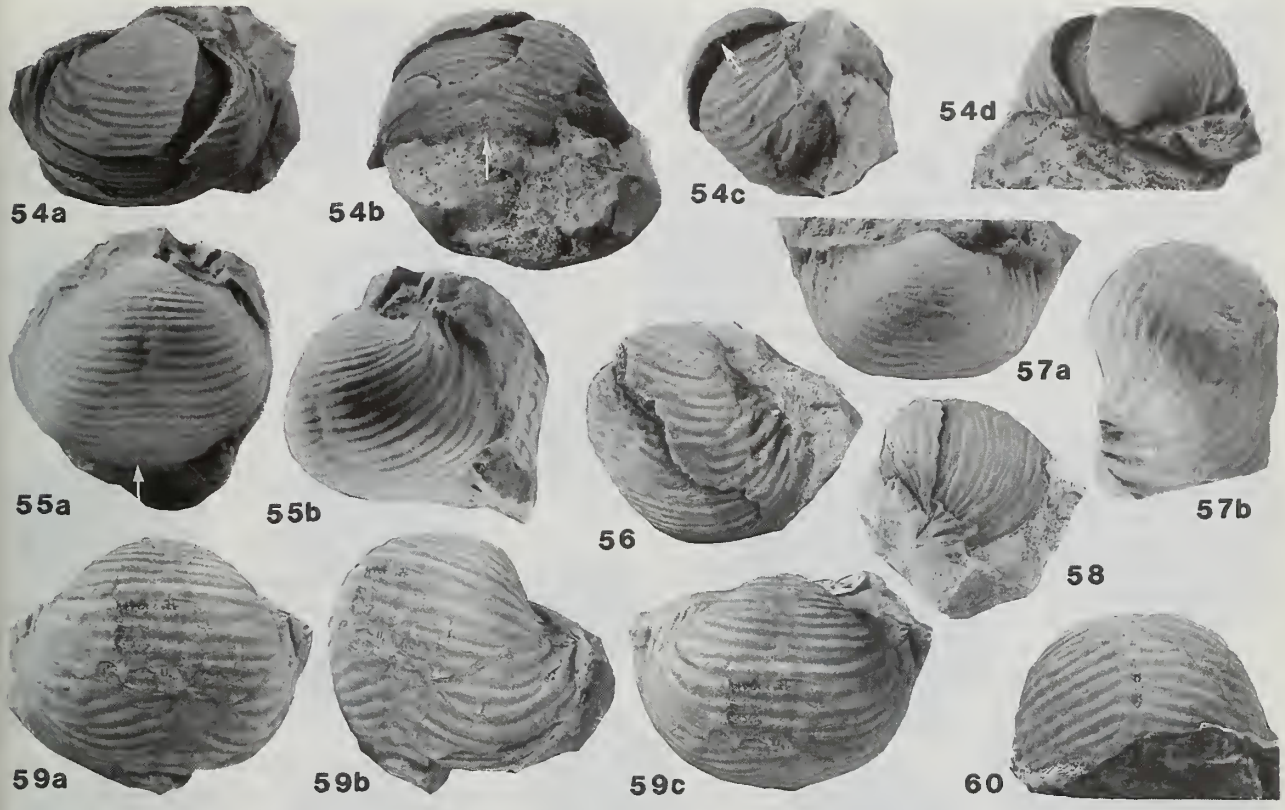
Figs 47–53 *Acanthoplecta mesoloba* (Phillips). Fig. 47, anterior view showing the slight outward turn of the valve margin indicating a gutter. Stebden Hill. BD1521. ×1. Figs 48a, b, dorsal and anterolateral views of a specimen showing the low median ridge within a shallow sulcus. Butter Haw Hill. BD1543. ×1·5. Figs 49a–c, a silicified dorsal valve from Co. Fermanagh viewed laterally and internally, showing the morphology and marginal gutter. BB52831. ×1·3. Fig. 50, an exfoliated dorsal valve interior showing the base of the cardinal process (arrowed) and parts of the gutter laterally. Stebden Hill. BD1531. ×1·5. Fig. 51, lateral view of a specimen from Bolland showing the spine bases on the flanks. BB61638. ×2. Figs 52a, b, **lectotype** (here selected), from the Gilbertson Collection, figured by Phillips (1836), viewed anteriorly and ventrally. The slight out-turn of shell at the ventral margin indicates a broken gutter. Bolland, Lancashire. B427. ×1·5. Figs 53a–c, dorsal, posterior and lateral views of an almost complete specimen showing flanking spine bases and dorsal valve dimples. Butter Haw Hill. BD1540. ×1·5.

AGE. All the Cracoe specimens collected by one of the authors (DJCM) came from late Asbian reef limestones containing goniatite assemblages indicative of B_{2b} zone age. None has been found in deposits of B_{2a} or P_{1a} age. It is considered likely that the four Cracoe specimens in the Garwood Collection of the British Geological Survey came from B_{2b} zone limestones. Eleven of the NHM specimens came from 'reefal' limestones of the Wetton and Narrowdale region of Staffordshire, or from Derbyshire, and are of the same age; two from Gilbertson's Bolland Collection could be of the same age, and the fourteenth is from J.S. Turner's Collection from the east side of Little Island, Cork, Ireland, where the rocks are also thought to be of late Asbian age. The Stoney Middleton specimen in the Sheffield City Museum is a possible exception, since rocks in the area could be Brigantian. However, as the specimen is so like all other Asbian specimens studied we conclude it also came from the Asbian rocks in the same region. It seems likely that *A. cracoensis* is confined to late Asbian reef limestone facies.

DESCRIPTION. Small (up to about 20 mm maximum width) thin-shelled plicatiferids with rounded, transversely oblong to depressed ovate, outlines when viewed dorsally. The lateral profile is strongly and evenly concavoconvex, but non-geniculate, and leaves a shallow body cavity. The ventral valve has a non-sulcate convex venter and trail, steep, slightly spreading flanks and reasonably well differentiated ears, which are flat and laterally tapering. The hinge line, including the ears, forms the widest part of the shell. The umbo projects only slightly beyond the hinge line. The dorsal valve closely follows the shape of the ventral valve, but the visceral area is flatter.

The ornamentation of both valves consists of distinct rounded rugae of consistent strength over the entire shell, other than the dorsal valve anteriorly where they are somewhat crowded and less well differentiated. Commonly there is a median deflection of the rugae posteriorly on the trail. Rugae increase, mainly on the flanks, by bifurcation and occasional intercalation; there are 6 or 7 rugae between 5 and 10 mm anteromedially from the ventral umbo. Spines are confined to the ventral valve, occurring on the crests of rugae and principally in two indistinct rows on the flanks and in a median row, associated with the flexure in the rugae on the trail. There are a few additional scattered spines. Growth lines are present on well-preserved valves.

Internal features are poorly known. In both valves there are weakly radial rows of tubercles and in ventral valves there



Figs 54–60 *Admodorugosus cracoensis* sp. nov. Figs 54a–d, **holotype** in ventral, anterior, lateral and posterior views. Note the shallow body cavity (arrowed), total rugation and median deflection of the ornamentation. Butter Haw Hill. BD2447. ×2. Figs 55a, b, ventral and ventrolateral views. Bolland, Lancashire. Gilbertson Collection, B439. ×2. Fig. 56, a specimen with its anterior ventral valve missing but showing some of the posterior spine bases. Wetton, Staffordshire. Davidson Collection, B5784/1. ×2. Figs 57a, b, ventral and anterolateral views of a specimen showing some delicate flanking spine bases. Wirksworth, Derbyshire. BD6577. ×2. Fig. 58, an incomplete specimen viewed laterally. ?Wetton, Staffordshire. Bateman collection (astutely labelled as 'undescribed'), Sheffield City Museum, [not numbered]. ×1·5. Figs 59a–c, anterior, anterolateral and ventral views of an almost complete specimen showing, despite a little shell damage, the characteristic deflection of rugae anteriorly. Wetton, Staffordshire. Davidson Collection, B5784/2. ×2. Fig. 60, an anterior view showing median spine bases. Wetton, Staffordshire. Davidson Collection, B5784/4. ×2.

are indications of a low ridge medially (e.g. B13811), separating the muscle fields. The dorsal valve has a low, sessile, strongly bilobed cardinal process (BD3350), as seen from the internal surface. There is a small alveolus and weak lateral ridges diverge slightly from the hinge line (e.g. BD2454, BD2456). There is no evidence of ear baffles.

Discussion. Although rather a rare species, it is distinctive and sufficient specimens have been accumulated to observe that in some the flanks are more widely spreading than in the other slightly narrower forms. Nearly half the specimens are somewhat exfoliated dorsal valves and, unless part of the ventral valve is also preserved, it is not always easy to recognize when the whole shell is not present. However, the lack of a projecting umbo, the relatively flat visceral disc and lack of any true spine bases should distinguish these dorsal valves.

Shape remained much the same during growth, between the observed widths of 12 mm to 21 mm, but, judging from growth lines, the ears became more prominent only during late stages of growth. Spines grew from the crests of rugae in a widely separated fashion, but there is a fairly distinctive median row of spines at about 4 mm intervals anteriorly and two rows each side extending anterolaterally from the umbo; one close to the hinge, at about 2 mm intervals, and the second following the curve of the flanks, at about 3 mm intervals. Clasping spines have not been seen but spines grew rarely at other positions on ventral valves only.

Admodorugosus cracoensis is typically levitusiinid in its rounded, strongly convex profile, rather shallow body cavity (Fig. 54c), median spines on a differentiated region of ventral valve ornament (the posterior deflection of the rugae), lack of any radial ribbing and lack of any dorsal ear baffles. Reasonably complete specimens cannot be confused with other contemporaneous species, but fragments resemble pieces of *Acanthoplecta mesoloba* (Phillips) or *Plicatifera plicatilis* (J. de C. Sowerby). The species, however, differs from *Levitusia* itself by being much smaller and in its fully rugose valves.

The complete covering of the shell by well differentiated rugae distinguishes *A. cracoensis* from other described *Acanthoplecta* or *Plicatifera* species; Carter's (1967) early Carboniferous *Acanthoplecta inopinata* from Texas, and *A. kirgisica* Galitzkaya 1977, from the early Viséan of Kurgisia, are both smooth trailed species.

The rugation is somewhat similar to that of *Fluctuaria*

undata (Defrance), but this species is more elongate in outline than *A. cracoensis* and the valves are ornamented entirely by well developed ribs. The entire ribbing and more numerous ill-defined rugae of *Undaria manxensis* Muir-Wood & Cooper 1960 distinguish this species.

It is noteworthy that ten NHM unnamed specimens collected by J. Tilsley from Thorpe Cloud, of Chadian age, resemble *Admodorugosus* in size and general shape. They differ in their less clearly defined rugae, which may not extend fully onto the trail, and in seeming to have rather deeper body cavities. Their spine distributions are similar, including those anteromedially, but their spines are somewhat more prominent anteriorly. These specimens resemble, but are distinct from, the Tournaisian early *Levitusia* species *L. hyperborea*, which occurs in Russia.

DISTRIBUTION. The 38 recognized specimens all came from the British Isles; from Staffordshire, Derbyshire, North Yorkshire and southernmost Ireland. The species has been recognized neither from literature nor in collections from rocks of the same age in the Isle of Man, nor from Belgium, where it might be expected in reef limestones containing otherwise similar assemblages.

Genus *GENICULIFERA* Muir-Wood & Cooper, 1960.

1960 *Geniculifera* Muir-Wood & Cooper: 187; pl. 47, figs 11–15.

TYPE SPECIES. *Avonia boonensis* Branson (1938), by original designation.

DIAGNOSIS. Small subcircular in outline. Dorsal visceral disc is almost flat and the strongly convex ventral valve produced a deep body cavity. Weak rugae occur posteriorly. No ribbing and sparse ventral spines.

DISCUSSION. The genus has not been described from the British Isles, other than the recent record from Treak Cliff, Derbyshire (Brunton & Tilsley 1991). Muir-Wood & Cooper (1960) included no species other than the type, which came from the Chouteau Limestone (early Mississippian = Tournaisian) of Missouri.

Geniculifera keyserlingiana (de Koninck, 1843)

Figs 61–71

1843 *Productus aculeatus* de Koninck (*non* Martin 1809 = Sowerby 1814): 200; pl. 10, fig. 8.
1847 *Productus keyserlingianus* de Koninck: 239; pl. 14, fig. 6.
1861 *Productus keyserlingianus* de Koninck; Davidson: 174; pl. 34, figs 15, 16.
1930 *Avonia keyserlingiana* (de Koninck); Muir-Wood: 106.

DIAGNOSIS. Ventral valve almost hemispherical in profile. Dorsal visceral disc about 10 mm wide, length shorter, almost flat and geniculate producing very deep body cavity and short trails. Slightly elongate swollen spine bases on ventral valve only, and long spines. No marginal structures and brachial impressions at 45° to hinge line.

TYPE SPECIMEN. Lectotype, here selected, specimen number R 50537(1) in the de Koninck collection, MNHN, Institut de Paléontologie, Paris (Figs 70a–c), from Visé, Belgium, probably of upper Viséan age.

MATERIAL. In the collections of the NHM there are about 40 specimens; most (23) come from Treak Cliff, Derbyshire. The DJCM collection contains 12 specimens, mainly from Elbolton, while 41 specimens from Stebden Hill are in the Liverpool Museum. There are two Davidson collection specimens in the NHM from the Settle area, significant through having been identified by de Koninck himself. In the Sheffield City Museum there are nine specimens, of which six are from Narrowdale. Settle material in the Burrows Collection, Sedgwick Museum, Cambridge, contains 21 specimens (E9618–39). The NHM collections from the Visé area of Belgium contain 17 specimens in the de Koninck collection, from where the species was first described, plus 7 others in old collections.

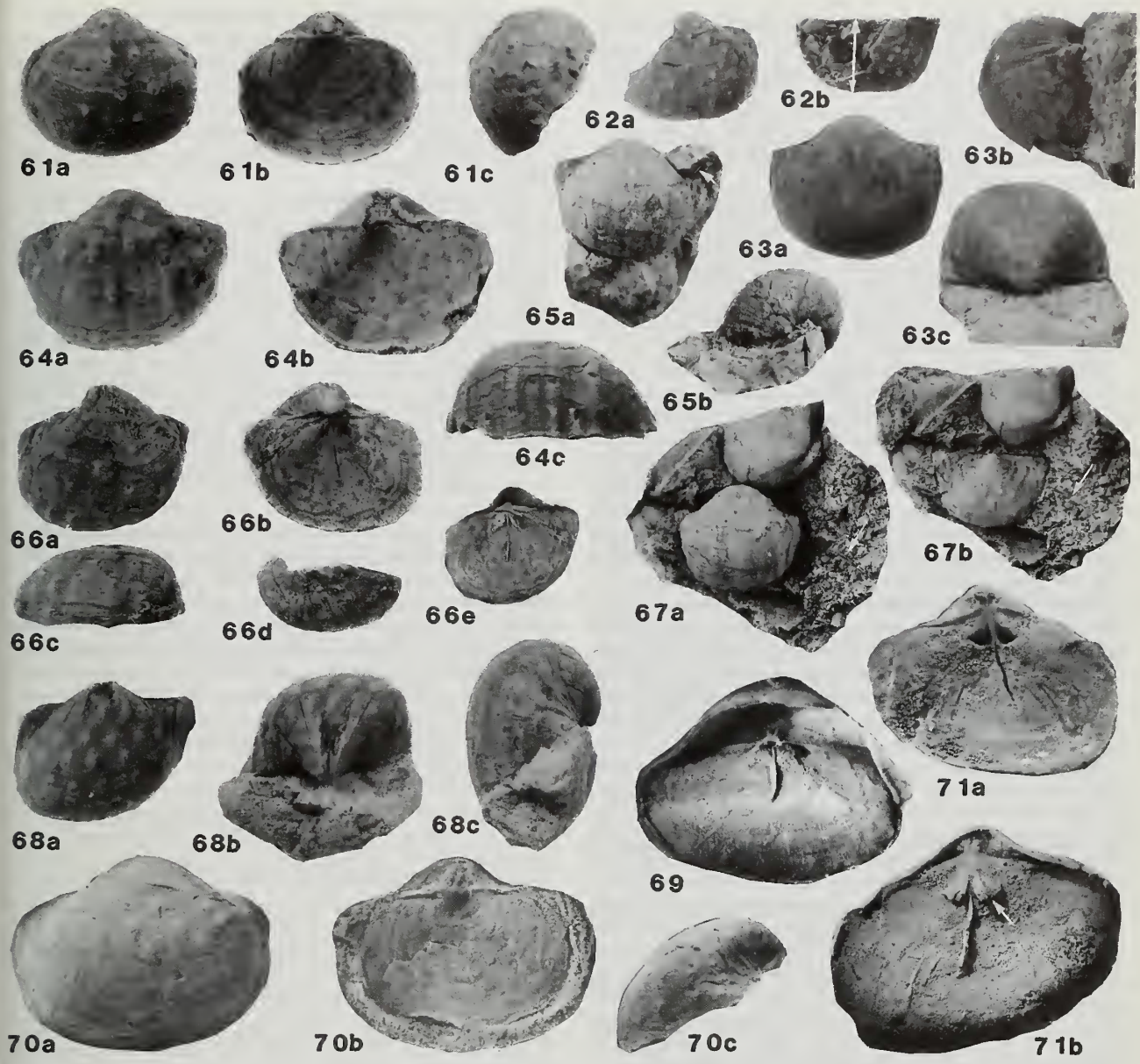
AGE. Upper Viséan, Asbian (B_{2a}, B_{2b}) and early Brigantian (P_{1a}).

DESCRIPTION. In outline the species is subrectangular, with the hinge line forming the widest part of the shell; the dorsal visceral disc is about 10 to 12 mm wide and 7 to 9 mm long. In profile the shell is almost planoconvex, the body part of the shell being almost hemisherical with simple trails reaching about 5 mm long. The umbo does not extend far beyond the hinge line and its flanks are not steep, so that the small ears are not strongly differentiated.

External ornanentation consists of relatively strong growth lines, weak irregular rugae posteriorly on most of the visceral region and spines on the ventral valve only, which arise from slightly elongate swollen spine bases. These are not necessarily associated with rugae, but tend to form a roughly quincuncial arragement with increasing separation anteriorly onto the trail. The spines are at high angles to the shell surface and may reach at least 7·5 mm long. Posteriorly, around the umbo, there are short, fine spines which appear to have been clasping. Dorsal valves have dimples, corresponding to the ventral spine positions, and geniculate quite strongly against the ventral valve. In a few large specimens a coarse costation developed along the trails.

Internally ventral valves have slightly raised elongate adductor scars reaching about 4·5 mm forwards from the umbo; the diductor scars spread fanwise anteriorly beyond the adductor scars. The swollen spine bases are visible internally and some of the flank and more anterior spines appear to have retained openings internally. Dorsal interiors have a sessile, separated, bilobed cardinal process, weakly supported laterally by slight cardinal ridges which do not extend into marginal structures. The adductor scars are well marked, commonly raised anteriorly and have triangular outlines. There is a weak median septum and brachial impressions extend from the adductor scars at about 45° anterolaterally. The internal surfaces of both valves have fine endospines.

DISCUSSION. De Koninck (1843) originally described the species as *P. aculeatus* Sow., but named it *keyserlingianus* in 1847. His descriptions and illustrations varied but significantly his earlier illustration (1843: pl. 10, fig. 8c) showed a section profile of the species displaying the very deep body cavity (see our Fig. 62b). Generally the 1847 illustrations are a little more accurate, but they give the false impression of a convex dorsal valve. Davidson's 1861 illustrations (pl. 34, figs



Figs 61–71 *Geniculifera keyserlingiana* (de Koninck). Figs 61a–c, ventral, dorsal and lateral views of a specimen figured by Davidson (1861: pl. 34, fig. 15). Settle, Yorkshire. Davidson Collection, B13818. ×2·5. Figs 62a, b, ventral and posterior views of an incomplete specimen showing the deep body cavity (arrowed). Elbolton. BD7563. ×1·5. Figs 63a–c, ventral, lateral and posterior views showing the high convexity of the ventral valve. Settle, Yorkshire. Davidson Collection, BB61545. ×2·5. Figs 64a–c, ventral, dorsal and anterior views of a specimen showing swollen spine bases and dorsal dimples. Skelterton Hill. BD7562. ×2·5. Figs 65a, b, ventral and lateral views of a specimen showing a spine extending into the rock (arrowed). Treak Cliff, Derbyshire. BD9332. ×1·5. Figs 66a–e, ventral, dorsal, anterior and lateral views of a partially exfoliated specimen (×2·5), and a latex cast taken from the dorsal interior (×2). Visé, Belgium. De Koninck Collection, B18242. Figs 67a, b, ventral view of a specimen on rock with a long spine (arrowed), and the same with the ventral valve removed showing a mould of the dorsal exterior. Treak Cliff, Derbyshire. BD9331. ×1·5. Figs 68a–c, ventral, posterior and lateral views of an internal mould showing swollen spine bases and raised ventral adductor muscle scars. Belgium. Natural History Museum (old collection) 97490. ×2·5. Fig. 69, latex cast taken from a specimen from Visé showing the dorsal interior in relation to the ventral umbo. Paris, R50537/2. ×3. Figs 70a–c, **lectotype** (here selected) in ventral, dorsal and lateral views. Note the flat dorsal valve and missing trail. The specimen has been slightly flattened. Visé, Belgium. Paris, R50537/.1. ×3. Figs 71a–b, dorsal view of an internal mould and a latex cast taken therefrom showing the raised adductor muscle scars (arrowed), cardinal process and brachial impressions. Visé, Belgium. Paris, R50537/3. ×3.

15, 16) of the species from Settle, Yorkshire, are good, although the dorsal internal mould illustrates brachial impressions in which the near horizontal component is over- accentuated (see our Figs 66e, 71a). In addition both de Koninck and Davidson rather over-stressed the swollen spine bases in their drawings. This feature is variable so their drawings are

good for some specimens, but commonly the swellings are much less prominent.

In the NHM there are over 20 specimens labelled *P. keyserlingianus* de Koninck from the Visé area of Belgium, but they are not all conspecific, some being another deep-bodied species, *Institifera tessellata* (de Koninck). These specimens are said to have been from the de Koninck collection, but his material became so widely spread, some of it *via* dealers, that it is difficult to be sure of provenance. No specimen closely resembles any of de Koninck's figures, but one registered as NHM 97490 is a good internal mould of the ventral valve. As the substance of the shell was thin the external morphology is also reasonably displayed (Fig. 68a), showing how some spines retained internal openings, as well as the ventral muscle fields.

The species differs from *Quasiavonia aculeata* (J. de C. Sowerby) in its deeper body cavity resulting from its virtually flat dorsal valve, in its slightly rugose posterior and in not having the somewhat lamellose growth lines characteristic of *Q. aculeata.* Another deep-bodied and similar-sized species is *I. tessellata,* but this species has an elongate outline, and more or less continuous coarse costae between which are concentrically arranged dimples. In addition *Institifera* has dorsal trails which curve inwards over the dorsal valve and outwards from the ventral valve, forming a rolled structure marginally.

The young of *Acanthoplecta* and *Plicatifera* differ from *G. keyserlingiana* in being relatively wider, less convex ventrally, and in having rugae which are better developed. The regular ventral convexity, deep body and size resemble *Eomarginiferina trispina,* but the lack of ribbing, poorly defined ears, numerous swollen spine bases and lack of internal marginal structures differentiate these species.

The type species of *Geniculifera, G. boonensis* (Branson, 1938) from Missouri, and another species *G. brevicula* Carter, 1967 from Texas, are late Tournaisian in age. These species differ from the British specimens in having rather flatter ventral valves so that the body cavity is slightly less deep and the valves bend rather more sharply between the visceral region and trails. The spine bases of the American species are less swollen and the frequency of spines greater in the Texas species. The assignment, therefore, of *keyserlingiana* to *Geniculifera* extends the range of that genus from the Tournaisian of North America to the upper Viséan of western Europe. At present the only other species known which is assigned to the genus from younger rocks is *G.* (?) *ukrainica* Aizenverg, 1983 from the Arnsbergian of the Ukraine.

PALAEOECOLOGY AND DISTRIBUTIONS

The species considered here, with the exception of *A. atripoides,* were free-living adults which lived epifaunally or quasi-infaunally, supported in the sediment by their shell surfaces and spines. In common probably with all other productidines, these species had an initial pediculate stage (a pedicle sheath has been described and figured on *Argentiproductus* and *Plicatifera* (Brunton 1965), but see also Figs 13a, b & Fig. 46b here), followed by clasping spines which augmented and secured the initial juvenile attachment; clasping spines have been observed on *Argentiproductus, Plicatifera, Acanthoplecta* and *Geniculifera.* With further growth, shells broke clear of their attachment surfaces and lived free on the substrate, stabilized and supported by various spine configurations. These adult free-living species occured in flank and bank facies within the Cracoean buildups with little or no obvious bathymetric selection between deeper or shallower water, but over a depth range of up to 120 m. Trivial numbers have, however, been located in the shallow water framework facies where they must have occupied sediment 'pools' within the framework.

Argentiproductus atripoides, in contrast, is unique to the framework facies (Table 1), occuring in significant numbers in this niche on the summit of Stebden Hill. Here the species formed part of a specialized shelly community which colonized the framework (stromatolite–sponge–bryozoan–coral framestone–bindstone), a community including shelly attached aulostegaceans (Mundy & Brunton 1985, Brunton & Mundy 1988*b*), chonopectinids (Brunton & Mundy 1986) and pseudomonotid 'oyster-like' bivalves. The adaptive strategy of *A. atripoides* was the continued growth of clasping spines (Fig. 21) beyond the juvenile stage, with the flank spine row (which typically is of ventrolateral support spines in free-living species) forming posteriorly directed attachment spines, somewhat suggestive of aulostegaceans. A further adaptation to the framework niche is the robust, thick shell with flattened profile, giving the species a superficial oyster-like form, a comparison which is all the more apparent when specimens occur directly with the pseudomonotids; this shell form would be well suited to the higher energy environment expected in this exposed niche. The species is also recorded from Glutton, Derbyshire, where similar patches of reef framework facies occur (Aitkenhead *et al.* 1985: fig. 9).

Table 1 Numbers and distribution of productellid and plicatiferid species in the Craven Reef Belt.

SPECIES	No.	Pres.%	Facies	Locations
Argentiproductus margaritaceus	131	19·1	F/B, (Fr)	1, 2, 6, 7, 8, 9, 10, 11, 12.
Argentiproductus atripoides	33	2·5	Fr	10.
Productina cf. *pectinoides*	15	3·1	F/B	8, 9.
Plicatifera plicatilis	128	9·2	F/B, (Fr)	1, 2, 6, 10, 11.
Plicatifera pseudoplicatilis	173	15·4	F/B, (Fr)	1, 2, 5, 6, 7, 8, 9, 10.
Acanthoplecta mesoloba	311	34·2	F/B, (Fr)	1, 2, 3, 5, 6, 7, 8, 9, 10, 11, 12.
Admodorugosus cracoensis	18	2·2	F/B	8, 9, 10.
Geniculifera keyserlingiana	76	7·8	F/B, (Fr)	1, 2, 5, 6, 8, 9, 10, 11, 12.

Notes:

Number Numbers of individuals recorded from initial collections of 20,941 brachiopods. As a result of preservational factors and some destructive analysis, not all the specimens have been retained in museum repositories.

Presence % Percentage occurrence of the species in 357 localities sampled.

Facies F/B = flank & bank; Fr = framework; (Fr) = very minor component.

Locations 1, High Hill; 2, Scaleber; 3, High South Bank; 4, Burns; 5, Cawden; 6, Wedber Brow; 7, Swinden; 8, Skelterton Hill; 9, Butter Haw Hill; 10, Stebden Hill, 11, Elbolton; 12, Thorpe Kail. See Brunton & Mundy 1988*b*: fig. 1.

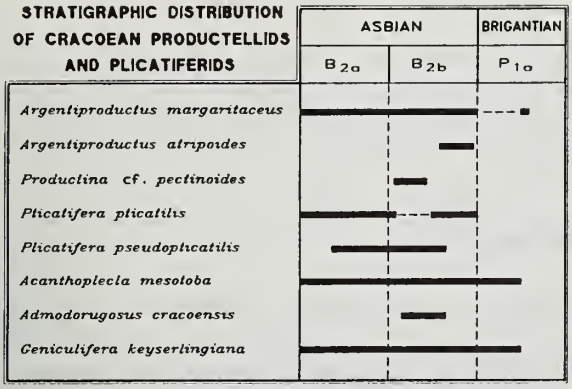


Fig. 72 The range of each species is based solely on their occurrence within the Craven Reef Belt and depends on goniatite calibration from the collections of DJCM (goniatite determinations by Dr W.H.C. Ramsbottom). Assemblage biozones of the *Beyrichoceras* Zone follow Riley (1990*a*).

The stratigraphical distributions of the productellid and plicatiferid species in the Craven Reef Belt, relative to the goniatite assemblage biozones, is shown in Fig. 72. *Argentiproductus margaritaceus, Acanthoplecta mesoloba* and *Geniculifera keyserlingiana* range throughout rocks of B_{2a} and B_{2b} Zone age and into P_{1a}. The latter two species are absent from strata of younger P_{1a} Zone age in which a low diversity, high abundance 'stressed' community (*Productus* community — Mundy, 1978, 1980) recolonized the buildups after a depositional hiatus, forming prolific shell beds on Stebden Hill and Elbolton. A single specimen of *Argentiproductus margaritaceus* has, however, been recovered from these beds.

Admodorugosus cracoensis typically occurs in strata of B_{2b} Zone age on Butter Haw and Skelterton Hill, as does *Productina* cf. *pectinoides*. The framework niche containing *Argentiproductus atripoides* on Stebden Hill is stratigraphically confined within strata interpreted as late B_{2b} Zone age.

Both *Plicatifera* species coexist in rocks of B_{2a} Zone age at Wedber Brow and High Hill, with *P. plicatilis* dominating, while in strata of early B_{2b} Zone age (well exposed on Butter Haw and Stebden Hill) *P. pseudoplicatilis* abounds with no record of *P. plicatilis*. In the overlying succession of late B_{2b} Zone age on Stebden Hill the latter species is again dominant, with insignificant numbers of coexisting *P. pseudoplicatilis;* in the Craven Reef Belt only *P. plicatilis* persists until the end of the B_{2b} Zone.

APPENDIX

The name '*Dorsirugatia*' was used, but not described, by Lazarev in 1990 (p. 80 & 145), where he placed it in the Productininae.

The full publication of *Dorsirugatia* Lazarev, 1992 took place while this paper was in preparation, and in a journal not easily obtained in Europe, so we add below the author's own description of the genus, type species and a brief discussion. This new Mongolian genus resembles *Productellina,* but until more of this British material becomes available the taxonomical relationships between the two must remain uncertain.

A NEW LATE DEVONIAN PRODUCTININID GENUS FROM MONGOLIA

Subfamily **PRODUCTININAE** Muir-Wood & Cooper, 1960
Genus ***DORSIRUGATIA*** Lazarev, 1992

1990 *Dorsirugatia* Lazarev: 80, 145.
1992 *Dorsirugatia* Lazarev, *in* Lazarev & Suursuren: 63.

DIAGNOSIS. Small Productininae with wide ears, an inflated ventral valve and weak ribbing starting on both valves anterior of the umbones; spines are rare with indistinct rows of up to three at bases of the flanks.

NAME. Latin, *dorsalis* = spinal or dorsal, *ruga* = wrinkle; referring to the ornamentation of the dorsal valve.

TYPE SPECIES. *D. tsagankhalgensis* Lazarev & Suursuren, 1992.

DISCUSSION. *Dorsirugatia* differs from *Productellina* in its more strongly inflated ventral valve (B=0·6 as compared to 0·9; see below), larger ears, wide but weak costation, and possibly also in having a row of about three spines at the bases of the flanks. *Dorsirugatia* differs from *Productina* and *Argentiproductus* by its weakly developed costation, which is lacking on the umbonal regions. *Dorsirugatia* may be the earliest member of the subfamily which subsequently evolved into two lineages, recognized in younger rocks as *Productina* and *Argentiproductus*. It is difficult to determine the exact age of *D. tsagankhalgensis,* but judging by the stage of development of the costation this species is slightly older than *Productellina fremingtonensis* Reed and ?*Dorsirugatia rjausakensis* Nalivkin (p.101).

Dorsirugatia tsagankhalgensis Lazarev & Suursuren, 1992. Figs 73–77

1992 *Dorsirugatia tsagankhalgensis* Lazarev & Suursuren: 63; pl. 15, figs 10–12.

NAME. The species is named after the mountain Tsagan-Khalgin-Ula.

DIAGNOSIS. As for genus.

TYPE SPECIMEN. Palaeontological Institute, Moscow, N3385/1523, a ventral valve (Figs 73a, b) from 2 km east of altitude point 2202 m at the foot of Mount Tsagan-Khalgin-Ula, Gobi Altai, Mongolia. Uppermost Tsagankhalgin Formation (= late Wocklumaria Zone), near the top of the Famennian, Upper Devonian.

MATERIAL. About 50 other dorsal and ventral valves from the type locality.

DESCRIPTION. Shells are 8–11 mm long and 13–16 mm wide. They are subtriangular in outline, but with a protruding ventral umbo. Greatest width is at the hinge. Ventral umbones are quite strongly inflated (B=0·6, see below), with no sulcus; a rounded umbo extends about 1·7–2·0 mm beyond the hinge; flanks spread at about 45° from the hinge and the ears are large and almost flat. The short trail may be slightly carinate. Costae are lacking at the umbo and ill-defined on the rest of the valve; their width is 0·5–0·7 mm (rarely up to 0·9 mm anteriorly) and they are simple, without branching or

Figs 73–77 *Dorsirugatia tsagankhalgensis* Lazarev & Suursuren. All from the type locality in Gobi Altai, Mongolia (see p.117). Figs 73a, b, the holotype viewed anteroventrally and posteroventrally showing the weak ribbing, which is lacking from the umbo. Palaeontological Institute, Moscow, 3385/1523. ×3. Fig. 74, a dorsal valve exterior showing the late stage ribbing and lamellae. Palaeontological Institute, Moscow, 3385/1514. ×3. Fig. 75, the external mould of a dorsal valve showing the weak rugae and bases of lamellae. BD9423. ×2. Figs 76a–d, anterolateral oblique view of a ventral valve exterior (×2), and the same in lateral, ventral and posterior views (×3). Arrows indicate spine bases. BD9421. Fig. 77, an anterolateral oblique view of an incomplete ventral valve and part of its internal mould showing tuberculation. BD9422. ×2.

additions. Ribs are lacking on the ears. Spines are sparse and confined to the ventral valve; their bases measure 0·2–0·3 mm in width. There are no spines at the hinge, but there is an indistinct row of up to three spines at the base of each flank; the first spine is at 3 mm from the beak, the second at 4–5 mm and the third at 7–7·5 mm. Dorsal valves are deeply concave and non-geniculate. The dorsal ornamentation is rugose and lamellose, with lamellae 0·2–0·4 mm wide posteriorly and wider anteriorly; thin growth lines may be visible. Costae are ill-defined and positioned anteriorly.

Internally the ventral muscle markings are shallow and indistinct; teeth are absent and internal surfaces are tuberculate. Ear baffles are low and broad, continuing anteriorly as weak marginal ridges. In dorsal valves the cardinal process is V-shaped, with no alveolus. The cardinal ridge is wide and indistinct.

(The B factors above, in relation to valve inflation, represent a logarithmic growth spiral in which low numbers indicate tighter spirals, i.e. greater inflation umbonally so that the ventral lateral profile is more strongly convex.)

REFERENCES

Aitkenhead, N., Chisholm, J.I. & Stevenson, I.P. 1985. Geology of the country around Buxton, Leek and Bakewell. *Memoir of the British Geological Survey*, London, Sheet **111**. x + 168 pp.

Aizenverg, D.E. 1983. [Upper Serpukhovian substage in the Donets Basin.] 161 pp., 88 pls. Kiev (Akademia Nauk Ukrainskoi SSR Institut Geologicheskikh Nauk) [In Russian].

Arthurton, R.S., Johnson, E.W. & Mundy, D.J.C. 1988. Geology of the country around Settle. *Memoir of the British Geological Survey*, London, Sheet **60**. ix + 147 pp.

Branson, E.B. 1938. Stratigraphy and paleontology of the Lower Mississippian of Missouri. *University of Missouri Studies. A Quarterly of Research*, Columbia, **13**. 205 pp.

Brunton, C.H.C. 1965. The pedicle sheath of productacean brachiopods. *Palaeontology*, London, **7**: 703–704.

—— 1966. Silicified Productoids from the Viséan of County Fermanagh. *Bulletin of the British Museum (Natural History)*, London, (Geol.), **12** (5): 175–243, 19 pls.

—— 1982. The functional morphology and palaeoecology of the Dinantian brachiopod *Levitusia*. *Lethaia*, Oslo, **15**: 149–167.

—— 1985. Some Carboniferous brachiopod distributions. *Compte Rendu. 10ème Congrès International de Stratigraphie et de Géologie du Carbonifère (Madrid 1983)*, **4**: 75–81.

—— & **Mundy, D.J.C.** 1986. Some Dinantian chonopectinid productaceans (Brachiopoda) from the British Isles. *Proceedings of the Yorkshire Geological Society*, Leeds, **46**: 1–10.

—— —— 1988*a*. The occurrence of the Lower Carboniferous linoproductid brachiopod *Vitiliproductus* Jin & Liao in Asia, the British Isles and Australia. *Proceedings of the Yorkshire Geological Society*, Leeds, **47**: 13–20.

—— ——1988*b*. Strophalosiacean and aulostegacean productoids (Brachiopoda) from the Craven Reef Belt (late Viséan) of North Yorkshire. *Proceedings of the Yorkshire Geological Society*, Leeds, **47**: 55–88.

—— & **Tilsley, J.W.** 1991. A check list of brachiopods from Treak Cliff, Derbyshire, with reference to other Dinantian (Lower Carboniferous) localities. *Proceedings of the Yorkshire Geological Society*, Leeds, **48**: 287–295.

Carter, J.L. 1967. Mississippian brachiopods from the Chappel Limestone of central Texas. *Bulletin of American Paleontology*, Ithaca, **53**: 251–488.

—— 1988. Early Mississippian brachiopods from the Glen Park Formation of Illinois and Missouri. *Bulletin of Carnegie Museum of Natural History*, Pittsburgh, **27**: 1–82.

Chao, Y.T. 1927. Productidae of China. 1. Producti. *Palaeontologia Sinica*, Peking, **B5**: 1–244.

Cooper, G.A. & Muir-Wood, H.M. 1951. Brachiopod homonyms. *Journal of the Washington Academy of Sciences*, **1**: 195–196.

Davidson, T. 1861. A monograph of British Carboniferous brachipods. *Palaeontographical Society (Monograph)*, London, **2**: 81–210.

Fredericks, G. 1928. Contributions to the classification of the genus *Productus*. *Izvestiya Geologicheskago Komiteta*, Leningrad, **46**: 773–792.

Galitskaya, A.Y. 1977. [*Early and Middle Carboniferous productids from north Kirgizia*. 168 pp., 64 pls. Frunze (Akademia Nauka Kirgizskoi SSR, Ordena Trudovogo Krasnogo Znameni Institut Geologii) [In Russian].

Gladchenko, A.Ya. 1955. [*Field atlas of the main brachiopods of the Lower Carboniferous of north Kirghiz*.] 30 pp., 28 pls, Table. Frunze (Akademia Nauk Kirgizskoi SSR, Institut Geologii) [In Russian].

— 1960. [*Brachiopods and stratigraphy of the Lower Carboniferous in the Son-Kul region of Kirghiz (central Tian-Shan)*.] 154 pp., 28 pls. Frunze (Akademia Nauk Kirgizskoi SSR, Institut Geologii) [In Russian].

Goldring, R. 1970. The stratigraphy about the Devonian-Carboniferous boundary in the Barnstable area of north Devon, England. *Compte Rendu. 6ème Congrès International de Stratigraphie et de Géologie du Carbonifère (Sheffield 1967)*, **2**: 807–816.

Gray, J.E. 1840. *Synopsis of the contents of the British Museum*. (42nd edn). 370 pp. London.

Gutteridge, P. 1990. The origin and significance of the distribution of shelly macrofauna in late Dinantian carbonate mud mounds in Derbyshire. *Pro-*

ceedings of the Yorkshire Geological Society, Leeds, **48**: 23–32.

Koninck, L. de 1843. *Description des Animaux Fossiles*. 650 pp. Liège.

—— 1847. *Recherches sur les animaux fossiles. I. Monographie des genres Productus et Chonetes*. 246 pp. Liège.

Lazarev, S.S. 1990. [Evolution and systematics of productids.] *Trudy Paleontologicheskogo Instituta*, Moscow, **242**: 1–173. [In Russian].

—— **& Suursuren, Sh.** 1992. [New productids (Brachiopoda) in the Carboniferous of Mongolia.] *In* Grunt, T.A. (ed.), [New taxa of fossil invertebrates of Mongolia]. *Trudy Sovmestnaya Rossiisko-Mongol'skaya Paleontologicheskaya Ekspeditsiya*, Moscow, **41**: 61–69, pls 14–16. [In Russian].

Martinez Chacon, M.L. 1979. Braquiopodos Carboniferos de la Cordillera Cantabrica. *Memorias del Instituto Geológico y Minero de España*, Madrid, **96**: 1–291.

McKellar, R.G. 1970. The Devonian productoid brachiopod faunas of Queensland. *Palaeeontological Paper, Geological Survey of Queensland, Brisbane*, **18**: 1–40.

Muir-Wood, H.M. 1928. The British Carboniferous Producti II. *Productus* (sensu stricto); *semireticulatus* and *longispinus* groups. *Memoirs of the Geological Survey of Great Britain, Palaeontology*, London, **3**: 1–217.

—— 1930. The Classification of the British Carboniferous brachiopod subfamily Productinae. *Annals and Magazine of Natural History*, London, (10) **5**: 100–108.

—— 1965. *In* Williams, A. *et al.* 1965.

—— **& Cooper, G.A.** 1960. Morphology, classification and life habits of the Productoidea (Brachiopoda). *Memoirs of the Geological Society of America*, Washington, **81**: 1–447.

Mundy, D.J.C. 1978. *In* McKerrow, W. S. (ed.), *The ecology of fossils*: 157–167. London.

—— 1980. *Aspects of the palaeoecology of the Craven Reef Belt (Dinantian), of North Yorkshire*. Unpublished Ph.D. thesis, Manchester University.

—— **& Brunton, C.H.C.** 1983. The discovery of the Dinantian productacean *Septarinia leuchtenburgensis* (de Koninck) in the British Isles. *Proceedings of the Yorkshire Geological Society*, Leeds, **44**: 333–340.

—— —— 1985. Morphological similarities in some British Dinantian and Texan Permian reef brachiopods. *Compte Rendu du 9ème Congrès International de Stratigraphie et de Geologie du Carbonifère (Urbana 1979)*, **5**: 225–232.

Nalivkin, D.V. 1979. [*Tournaisian brachiopods of the Urals*.] 247 pp., 65 pls. Leningrad. 'Nauka' (Otdelenie Geologii, Geofiziki, Geochimii) [In Russian].

Paeckelmann, W. 1931. Die brachiopoden des deutschen Unterkarbons, 2: Die Productinae und Productus-ahnlichen Chonetinae. *Abhandlungen der Preussischen geologischen Landesanstalt*, Berlin, **136**: 1–352.

Pareyn, C. 1962. Les massifs carbonifère du Sahara sud oranis. *Publications du Centre de Recherches Sahariennes*, Paris, (Sér. Géol.) **1**. 2, Paléontologie stratigraphique. 244 pp.

Paul, M. 1942. *Thomasella* n. nom. = *Thomasina* Paeckelmann, 1931. (Brachiop. Productidae). *Zentralblatt für Mineralogie, Geologie und Paläontologie*, Stuttgart, (B) **1942** (6): 191.

Phillips, J. 1836. *Illustrations of the geology of Yorkshire: 2, The Mountain Limestone District*. 235 pp. London.

Poletaev, V.I., Brazhnikova, N.E., Vasilyuk, N.P. & Vdovenko, M.V. 1991. Local zones and major Lower Carboniferous biostratigraphic boundaries of the Donets Basin (Donbass), Ukraine, USSR. *In* Brenckle, P.L. & Manger, W.L. (eds), Intercontinental Correlation and Division of the Carboniferous system. Contributions from the Carboniferous Sub-commission Meeting, Provo, Utah, 1989. *Courier Forschungsinstitut Senckenberg*, Frankfurt A.M., **130** :47–59.

Reed, F.R.C. 1943. Notes on certain Upper Devonian brachiopods figured by Whidborne. *Geological Magazine*, Hertford, **80**: 95–106.

Riley, N.J. 1990*a*. Revision of the *Beyrichoceras* Ammonoid-Biozone (Dinantian), NW Europe. *Newsletters on Stratigraphy*, Leiden, **21**: 149–156.

—— 1990*b*. Stratigraphy of the Worston Shales Group (Dinantian), Craven Basin, north-west England. *Proceedings of the Yorkshire Geological Society*, Leeds, **48** :163–187.

Roberts, J. 1963. A Lower Carboniferous fauna from Lewisbrook, New South Wales. *Journal of the Proceedings of the Royal Society of New South Wales*, Sydney, **97**: 1–31.

—— 1971. Devonian and Carboniferous brachiopods from the Bonaparte Gulf Basin, northern Australia. *Bulletin of the Bureau of Mineral Resources, Geology and Geophysics, Australia*, Melbourne, **122**: 1–319.

—— 1976. Carboniferous chonetacean and productacean brachiopods from eastern Australia. *Palaeontology*, London, **19**: 17–77.

Rodriguez, J. & Gutschick, R.C. 1968. *Productina, Cyrtina*, and *Dielasma* (Brachiopoda), from the Lodgepole Limestone (Mississippian) of southwestern Montana. *Journal of Paleontology*, Tulsa, **42**: 1027–1032.

Rotaï, A.P. 1939. Nizhnii Karbon Donetskogo basseiina i polozhenie namyurskogo yarusa v Kamennougol'noi sisteme. [Le Carbonifère Inférieur du Bassin du Donetz et la position du Namurien dans le Système Carbonifère.] *Trudy XVII Sessii, Mezhdunarodnyi Geologicheskii Kongress 1937*, Moskva, **1**: 465–478 [*Report of the XVII Session, International Geological Congress 1937*, Moscow, **1**: 461–474] (In Russian and French).

Schuchert, C. & Le Vene, C.M. 1929. Brachiopoda (Generum et Genotyporum Index et Bibliographia). *Fossilium Catalogus*, Berlin, (1, Animalia) **42**: 1–140.

Sowerby, J. de C. 1824. *The Mineral Conchology of Great Britain*, **5**: 63–138. London.

Sutton, A.H. 1938. Taxonomy of Mississippian productidae. *Journal of Paleontology*, Tulsa, **12**: 537–569.

Thomas, I. 1914. The British Carboniferous Producti, 1. Genera *Pustula* and *Overtonia*. *Memoirs of the Geological Survey of Great Britiain, Palaeontology*, London, **1** (4): 197–366, 4 pls.

Timms, A.E. [1978.] *Aspects of the palaeoecology of productid 'reef' limestones in Derbyshire*. Unpublished Ph.D. thesis, Manchester University.

—— **& Brunton, C.H.C.** 1991. Growth rates and periodicity in *Antiquatonia* and *Plicatifera*, Lower Carboniferous productacean brachiopods. *In* MacKinnon, D.I., Lee, D.E. & Campbell, J.D. (eds), *Brachiopods through time:* 41–47. Rotterdam.

Warren, P.T., Price, D., Nutt, M.J.C. & Smith, E.G. 1984. Geology of the country around Rhyl and Denbigh. *Memoir of the British Geological Survey*, London, sheet **95** & **107**. x + 217 pp.

Weller, S. 1909. Kinderhook faunal studies. V. The fauna of the Fern Glen Formation. *Bulletin of the Geological Society of America*, New York, **20**: 265–332.

Whidborne, G.F. 1897–98. The Devonian fauna of the south of England. *Palaeontographical Society (Monograph)*, London, **3** (2–3): 113–236.

Williams, A. et al. 1965. *Treatise on Invertebrate Paleontology*, H. *Brachiopoda*. 927 pp. Lawrence, Kansas.

Winchell, A. 1863. Descriptions of fossils from the yellow sandstones lying beneath the 'Burlington Limestone' at Burlington, Iowa. *Proceedings of the Academy of Natural Sciences of Philadelphia*, **7**: 2–25.

Winkler Prins, C.F. 1968. Carboniferous Productidina and Chonetidina of the Cantabrian Mountains (NW Spain): systematics, stratigraphy and palaeoecology. *Leidse Geologische Mededelingen*, **43**: 41–126.

Zakowa, H. 1985. Some Productidina (Brachiopoda) from the Upper Visean of Galezice. *Kwartalnik Geologiczny*, Warsaw, **29**: 301–328.